January 2014

Songbird Response To Mixed Ungulate Herd Reduction Through Changes In Vegetation At Sullys Hill National Game Preserve

Bethany J. Walters

SONGBIRD RESPONSE TO MIXED UNGULATE HERD REDUCTION THROUGH CHANGES IN VEGETATION AT SULLYS HILL NATIONAL GAME PRESERVE

by

Bethany J. Walters
Bachelor of Science, University of Minnesota, 1988, 2012

A Thesis

Submitted to the Graduate Faculty

of the

University of North Dakota

in partial fulfillment of the requirements

for the degree of

Master of Science

Grand Forks, North Dakota
December
2014

This thesis, submitted by Bethany Walters in partial fulfillment of the requirements for the Degree of Master of Science from the University of North Dakota, has been read by the Faculty Advisory Committee under whom the work has been done and is hereby approved.

Dr. Susan Ellis-Felege

Dr. Robert Newman

Dr. Daniel Svedarsky

This thesis is being submitted by the appointed advisory committee as having met all of the requirements of the School of Graduate Studies at the University of North Dakota and is hereby approved.

Wayne Swisher
Dean of the School of Graduate Studies

12-8-14
Date

PERMISSION

Title: Songbird response to mixed ungulate herd reduction through changes in vegetation at Sullys Hill National Game Preserve

Department Biology

Degree Master of Science

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of North Dakota, I agree that the library of this University shall make it freely available for inspection. I further agree that permission for the extensive copying for scholarly purposes may be granted by the professor who supervised my thesis work or, in her absence, by the Chairperson of the department or the dean of the School of Graduate Studies. It is understood that any copying or publication or other use of this thesis or part thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of North Dakota in any scholarly use which may be made of any material in my thesis.

Bethany Walters
December 2014

TABLE OF CONTENTS

LIST OF TABLES vii

LIST OF FIGURES xi

ACKNOWLEDGMENTS xii

ABSTRACT xv

CHAPTER

I. BACKGROUND AND LITERATURE REVIEW: UNGULATE, AVIAN, AND FOREST ECOLOGY 1

INTRODUCTION 1

UNGULATE ECOLOGY 2

AVIAN ECOLOGY 8

FOREST ECOLOGY 11

STUDY OBJECTIVES AND HYPOTHESIS 12

STUDY APPROACHES 14

LITERATURE 16

II. FOREST REGENERATION RESPONSE TO MIXED UNGULATE REDUCTION AT SULLYS HILL NATIONAL GAME PRESERVE, A TEMPERATE DECIDUOUS FOREST: IS SEEDLING RECRUITMENT WITHOUT RETURN OF SPECIES RICHNESS ENOUGH? 31

ABSTRACT 31

INTRODUCTION 32

METHODS 34

RESULTS 37

DISCUSSION 39

MANAGEMENT IMPLICATIONS 45

LITERATURE CITED 47

III. PASSERINE RESPONSE TO CHANGES IN FOREST VEGETATION RESULTING FROM REDUCTION OF A MIXED UNGULATE HERD 71

ABSTRACT 71

INTRODUCTION 72

METHODS 74

RESULTS 78

DISCUSSION 82

MANAGEMENT IMPLICATIONS 88

LITERATURE CITED 90

IV. CONCLUSIONS AND MANAGEMENT IMPLICATIONS 116

LITERATURE CITED 123

APPENDICES 130

LIST OF TABLES

Table Page

1. Four forest habitat-treatment combinations found at SHNGP, their respective sizes and proportion of total area they represent 58

2. Animal Unit Month Conversion Table 59

3. Common names, abbreviations, and scientific names of shrubs and trees measured at SHNGP. 60

4. Summary statistics of tree species for each of four habitat-grazing combinations at SHNGP 61

5. Summary statistics for shrub species at each of four habitat-grazing combinations at SHNGP 62

6. Model selection using AICc for stem density at 65 points relative to predictors of habitat (upland or bottomland), treatment (grazed/browsed or reference), and year (2005, or 2012). K is number of parameters, and w_i is Akaike weights....63

7. Model-averaged estimates for binary covariates of Treatment, Year, Habitat, and Dispersion explaining stem density at Sullys Hill National Game Preserve. 64

8. Summary statistics for individual-based sampling of tree species using asymptotic estimators....65

9. Descriptions of vegetation covariates used in models of abundance and detection....97

10. Number of birds observed based on maximum counts for each species at each point....99

11. Abundance models constructed using from 2004, 2012, and 2013 100

12. Model-averaged detection, r, estimates for before-after herd reduction models using covariates of treatment (grazed, ungrazed, exclosure), year (2004, 2012, 2013) and habitat (upland, bottomland) for four target bird species 101

13. Model-averaged parameter estimates describing the relationship between abundance and covariates of year (2004, 2012, 2013), habitat type (upland, bottomland), and treatment (grazed, ungrazed, exclosure) 102

14. Model-averaged estimates of abundance and detection based on top 95% of all models for each target bird species based on grazing treatment (grazed, ungrazed, exclosure), year (2004, 2012, 2013), and habitat type (upland, bottomland) 103

15. Top 95% of candidate models constructed using bird abundance data from 2012 and 2013 104

16. Model-averaged estimates of detection, r, based on top 95% of models constructed using vegetation covariates and bird abundance 106

17. Model-averaged beta (β) estimates for covariates explaining abundance 107

18. Model-averaged estimates for abundance and detection based on top 95% of all models for each target bird species and based on vegetation and habitat covariates 109

19. Asymptotic estimator summary statistics for individual-based sampling of birds at SHNGP using Chao estimators (see Gotelli and Ellison 2013, and Chao et al. 2009) 109

20. Parameter estimates and 95% confidence interval (CI) for all eleven models used to evaluate stem density. 131

21. Abundance models constructed using ovenbird abundance data from 2012 and 2013 133

22. Abundance models constructed using yellow warbler data from 2012 and 2013 134

23. Abundance models constructed using American redstart data from 2012 and 2013 135

24. Avian species with alpha codes, common name, and scientific name and presence (x) or absence (0) in 2004, 2012, and 2013 136

25. Incidental avian sightings at Sullys Hill National Game Preserve, not observed at survey points.....138

26. Abundance models based on red-eyed vireo 2012/2013 data…….....……...139

LIST OF FIGURES

Figure Page

1. Timeline of major monitoring and management events at Sullys Hill National Game Preserve 29

2. Plant-animal interactions. 30

3. U.S. Fish and Wildlife survey counts of bison, elk, and deer since reintroduction in 1917....66

4. Seventy forest survey points collected across Sullys Hill National Game Preserve in 2005 and 2012. 67

5. Individual-based woody species accumulation curves for grazed and ungrazed upland habitats at SHNGP....68

6. Individual-based woody species accumulation curves for grazed and ungrazed bottomland habitat at SHNGP....69

7. Boxplots of tree and shrub stem density for each habitat type and year....70

8. Avian point count survey locations at Sullys Hill National Game Preserve in North Dakota, 2012 – 2013....110

9. Understory metrics separated by habitat type for a) litter depth (cm), b) native sedges and non-native graminoids (Kentucky bluegrass and smooth brome) and c) percent vegetation for each habitat type....111

10. Midstory vegetation metrics of a) percent vegetation coverage at midstory level, and b) number of woody species at midstory level in each habitat type....112

11. Canopy vegetation metrics of a) number of tree species in canopy of each habitat type, and b) percent canopy closure by habitat type....113

12. Individual-based species accumulation curves for bird species in upland and exclosure habitat type and year (n=4)....114

13. Individual-based species accumulation curves for bird species in bottomland habitat type and year (n=4) 115

14. Percent of diet of each vegetation across four seasons of sampling (Bertie and Sweitzer unpublished data) 129

ACKNOWLEDGMENTS

I am sincerely grateful for all the time, effort, and guidance my advisory committee has given me these past two years. Dr. Susan Felege and Dr. Robert Newman have patiently explained statistical techniques, model interpretation, and the scientific writing used to explain our project. Dr. Susan Felege spent many long hours editing my thesis and I am thankful for her input; she has greatly improved the tone and professionalism of this paper. Dr. Daniel Svedarsky has offered excellent insight into the scientific process and the role of plant communities. University of North Dakota faculty, Dr. Brett Goodwin, and Dr. Kathryn Yurkonis, have also taken time to increase my understanding of methods and programs, all of which have been used in this thesis.

I am also appreciative of the opportunity to conduct this project at Sullys Hill National Game Preserve and for the housing, equipment, and support, and feedback provided by the US Fish and Wildlife Service biologist, Mark Fisher. He not only helped me understand some of the large ungulate dynamics at Sullys Hill National Game Preserve, but he also shared biological technicians from his other projects to help me meet seasonal deadlines.

There is a long list of graduate and undergraduate students I wish to thank for helping with data entry, biometry, GIS mapping, artwork, and field work: Dustin Van Thuyne, Nick Kludt, Paul Burr, Leila Mohsensian, Amanda Saul, Jasmine Lorenz, David Remmen, Sarah Pederson, Brandon Hanson, and Trevor Green.

I wish to acknowledge the following agencies for providing the funding that made this project possible: University of North Dakota, Department of Biology, UND Graduate school, North Dakota EPSCoR program, and US Fish and Wildlife, Devils Lake WMD – DBR Program. North Dakota EPSCoR program also provided funding for travel, allowing me to present results at national and state Wildlife Society conferences.

To my original mentors, Dr. Bill Faber and Mr. Gary Carson,
The first to inspire me to sound conservation action through thorough scientific inquiry.

ABSTRACT

Big game management traditionally focused on single species management with less emphasis, until recently, on community interactions. Sullys Hill National Game Preserve (SHNGP) is a 678 hectare preserve where extirpated Plains bison (*Bison bison*) were reintroduced along with Rocky Mountain elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*). These large ecosystem engineers have been managed at varying densities within a fenced area of deciduous woods, wetlands, and native prairie since 1918. Grazing, browsing, and rubbing by ungulates, along with additional refuge management prescriptions (e.g. prescribed fire), shape the understory and midstory and in turn determine which birds will nest and forage in the area. The 2008 SHNGP Comprehensive Conservation Plan recommended a 50% reduction in herd sizes based on vegetation surveys which indicated little forest regeneration. The suspected cause was overbrowsing by ungulates. An ungulate density of 37 ungulates/km^2 was reduced to 19 animals/km^2. This density has been annually maintained since 2008. The primary objective of this study was to determine if large ungulate reduction has improved forest regeneration with an ensuing increase in bird abundance and diversity. Vegetation and avian surveys were conducted pre-treatment (before herd reduction) and repeated post-treatment in 2012-2013.

Repeat forest surveys revealed a return of regeneration when analyzed using negative binomial regression, but regeneration is lower in grazed areas as compared to ungrazed. Species accumulation curves revealed that species richness is not returning in pace with regeneration in grazed habitat for both upland and bottomland habitat types.

Repeat bird surveys of four target species, ovenbirds (*Seiurus aurocapilla*), yellow warblers (*Dendroica petechia*), American redstart (*Setophaga ruticilla*), and red-eyed vireos (*Vireo olivaceus*) were analyzed for changes in abundance using Royle repeat measures and changes in species diversity using species accumulation curves. Changes in target bird density before and after the herd reduction treatment revealed lower abundance and downward trends in ovenbird. No significant changes in abundance were observed in yellow warblers, American redstarts or red-eyed vireos, but yellow warblers and redstarts had higher abundance in exclosure (100% ungulate reduction) than grazed (50% ungulate reduction) and were similar to ungrazed abundance.

Bird abundance relative to post-herd reduction vegetation was analyzed to determine if there were specific associations with species or guilds which may be impacted by herd reduction. We found that ovenbird abundance is higher with midstory basswood saplings and native sedges and lower with native forbs. Yellow warblers had higher abundance with native sedges and lower with more midstory cover. American redstarts had higher abundance with deeper litter and lower abundance with midstory ash saplings. We found no specific vegetation associations for red-eyed vireos. Some of the associations were weakly significant and all surveys conducted at one site so there was no replication for increased inference. We concluded that more time, more browser reduction, and additional disturbance techniques may be needed to improve forest vegetation recovery and associated increases in bird abundance.

CHAPTER I
BACKGROUND AND LITERATURE REVIEW: UNGULATE, AVIAN, AND FOREST ECOLOGY

INTRODUCTION

Sullys Hill National Game Preserve (SHNGP), established in 1904 by President Theodore Roosevelt, is a unique mosaic of lacustrine wetlands, deciduous forests, and native prairie within the Prairie Pothole Region of North Dakota. By 1918 extirpated Plains bison (*Bison bison*; hereafter bison*)* were reintroduced along with Rocky Mountain elk (*Cervus elaphus*; hereafter elk) and white-tailed deer (*Odocoileus virginianus;* hereafter deer) in an effort to preserve some of the wildlife that was a part of North Dakota history (USFWS 2008). Three primary management goals were established in 2008 (USFWS 2008): 1) maintain a healthy forest with various age classes and structure; 2) manage for healthy populations of bison, elk, migratory birds and indigenous wildlife; and 3) provide interactive education and visitor service facilities for the public. In an effort to follow these three goals, many changes occurred over the next century to manage the ungulate herds and land of SHNGP (Figure 1).

The 1986 SHNGP big-game management plan called for a bison herd of 25 – 40 animals, an elk herd of 15 – 25 animals, and a deer herd of 10 – 30 animals or a maximum density of 37 ungulates/km^2 (Veikley 1984). In early 2000s, overgrazing was suspected and changing vegetation were thought to be impacting bird densities on SHNGP. Since only two percent of North Dakota is wooded, hardwood forests and their subsequent bird and animal communities are a distinctive resource on the prairie landscape. The forests of SHNGP create a unique birding oasis attracting many of the 60,000 annual visitors (USFWS 2008).

In 2005 an investigation into the health of the forest included forest vegetation surveys. At that time, foresters from the North Dakota Forest Service discovered that there was no regenerative growth, meaning that the forest was not replacing itself and was, in essence, dying. In response to the lack of regeneration, the North Dakota Forest Service (Harsel 2005) and the University of North Dakota (Bertie and Sweitzer 2008) made recommendations to improve the health of the forest. These recommendations included culling the ungulate herd size by roughly 50% for all three species and adding exclosures (i.e., areas within the grazed section that are fenced off to allow the vegetation to "rest" from grazing and browsing). In 2008 a new Comprehensive Conservation Plan (CCP) included herd reductions and maintenance recommendations as follows: ≤20 bison, <20 elk, <20 deer or a maximum density of 19 ungulates/km^2. Decreased herds have been annually maintained since 2008 (USFWS 2008). The 2008 CCP called for re-evaluation of the forest health and wildlife community in 2012 and is the motivation behind this study.

UNGULATE ECOLOGY

Large ungulates such as bison, elk, and, to a lesser extent, deer, are ecosystem engineers when at a healthy density (Jones et al. 1997). They have the potential to change vegetative structure and composition which in turn impacts other animals dependent on that vegetation, such as birds (Figure 2). These changes result in landscape heterogeneity which increases diversity of the animas dependent on that vegetation. Each ungulate has a different, yet often overlapping, role in forest dynamics at SHNGP.

Plains Bison (*Bison bison bison)*: Plains bison traditionally occurred as free ranging herds on the open landscape of the prairie. While this is historically true, bison also used forested habitats for cover in harsher climate conditions and for isolation during calving (Larter and Gates

1991, Campbell et al. 1994). In the late1800s near extermination of bison resulted from over-exploitation by market hunters for meat and fur trades (Isenberg 2000). Conservation efforts have allowed a return of bison and current populations are greater than 500,000 across North America (Boyd 2003). However, only three percent are free-ranging on preserves or in conservation management based herds, and the rest are privately owned and raised for commercial use (Feldhamer et al. 2003). Since many herds are now held in fenced areas with mixed habitats of woodlands, wetlands, and grasslands, effects of bison on ecological communities must be assessed to determine if other animal or habitat management goals are being maintained. Two potential impacts of bison presence at SHNGP include: direct changes in forest vegetation structure and composition as a result of browsing, rubbing, and horning and indirect changes in forest vegetation structure and composition as a result of soil compaction from large ungulate hoof disturbances or changes due to browse altered vegetation communities.

Plains bison graze on grasses and sedges almost exclusively with little use of forbs or shrubs in summer, but make use of woody shrubs as browse in winter (Larter and Gates 1991, Knapp et al. 1999). Nutritional quality, plant phenology, snow depth, and water availability are primary drivers for bison food choices and subsequent movement through an area (McHugh 1958, McNaughton 1990, Larter and Gates 1991, Plumb and Dodd 1993, Bailey et al. 1996, Fortin et al. 2003). Bison selection of grasses and sedges allows more tree seedlings to survive by decreasing competition for nutrient resources, but at the same time seedlings and saplings serve as a source of browse in winter (Peden 1976, Reynolds et al. 1978, Coppedge et al. 1998, Coppedge and Shaw 1998, Fortin et al. 2003).

Furthermore, bison destroy midstory by horning and rubbing or scratching during the summer. It is hypothesized that bison rub and horn vegetation to remove shedding pelage and

possibly as relief from insects. Coppedge and Shaw (1997) documented damage to approximately 29% of the midstory by the bison at a density of 2.5 animals/km^2, demonstrating the potential impacts bison can have on forest structure.

Male bison may reach an adult mass of 907 kg and female up to 545 kg (Seabloom 2011). Studies have shown that large ungulates such as bison and cattle affect ecosystems through soil compaction. Specific studies of bison static ground pressure have not been conducted, but studies of mature cattle provide approximate hoof-bearing pressures of 1.7 kg/cm^2. This is roughly equivalent to a heavy wheeled tractor and can affect bulk density of soil to a depth of one meter (Bezkorowajnyj et al. 1993). Soil compaction of topsoil and upper horizons affects plant growth in three ways: suppressed root elongation, changes in soil fauna which affect decomposition and nutrient cycling, and through changes in hydrology (Ferrero 1991, Whalley et al. 1995, Belsky and Blumenthal 1997, Hamza and Anderson 2005). Roots elongate or push through soil to find nutrients, water, and to stabilize above ground vegetation structure. If soil is compacted by increased downward pressure or weight, the soil structure is compressed, and it is much more difficult for plant roots to push through soils. This slows plant growth both below and above ground (Whalley et al. 1995, Hamza and Anderson 2005).

In addition to slowing plant growth, compacted soil also affects soil fertility. Soil fertility depends on the presence of earthworms and microorganisms. Earthworms feed on organic matter and aerate the soil. Compaction of soil can kill earthworms (Whalley et al. 1995). Lower numbers of earthworms will cause a decline in soil fertility and an increase in bulk density of soil which leads to decreased water infiltration rates. Oxygen content decreases at depth with compacted soil which, in turn, affects soil microbes and subsequently affects nutrient cycling and

nitrogen loss, both important factors in soil fertility which is a driver of forest health (Bezkorowajnyj et al. 1993, Whalley et al. 1995, Belsky and Blumenthal 1997).

Soil infiltration, or the rate that water penetrates the soil surface, determines how much water enters the soil ecosystem and how much ends up as runoff. Bison can alter the rates of infiltration by reducing vegetative ground cover and litter through grazing and compaction. Lower soil moisture yields reduced plant productivity which further degrades soil structure. Decreased ground water also can cause increases in tree mortality during dry cycles (Bezkorowajnyj et al. 1993, Belsky and Blumenthal 1997).

Bison can also compact the soil through wallowing. Thus, a positive aspect of bison-induced soil compaction from wallowing is the formation of ephemeral ponds. Wallows hold water and provide breeding habitat for anurans (Gerlanc and Kaufman 2003) and aquatic invertebrates (Keeley and Zedler 1998). Wallows produce moist substrate for drought intolerant plant species (Polley and Collins 1984), and provide colonization sites for pioneering and ephemeral species (Collins and Uno 1983). The landscape effect is increased habitat heterogeneity (Polley and Wallace 1986, Knapp et al. 1999, McMillan et al. 2011).

Bison spend part of their spring and summer moving between open grassland areas and forested areas for cover and grazing. There are no studies to date that quantify the amount of time bison will spend in each habitat type so it is unclear how much of an effect bison may have on forested habitats. Proximity to water has been shown to dictate some of the grazing patterns, especially during summer months (Kohl et al. 2013). Forest cover for relief of heat or wind is also a driver for movement between open and forested habitats. With herds that forage for food during the winter, browse may play a larger role, but the SHNGP herds are supplemented with alfalfa hay during the winter months and this will decrease foraging effects on vegetation

(Kowalczyk et al. 2011, Bertie and Sweitzer Unpublished). Supplemental feeding is currently being reviewed by SHNGP management staff given the potential for disease transmission (Smith 2013).

Rocky Mountain Elk (*Cervus elaphus nelsoni*): Wapiti or elk are large even-toed ungulates that weigh about 15 kg at birth. Adult bulls have an average weight of 333 kg and can reach >400 kg (Feldhamer et al. 2003). Adult females average approximately 80% of adult bull weights. Elk browse on a mixture of vegetation that includes grasses, forbs, and shrubs, but is dominated by sedges (Christianson and Creel 2007). Elk will forage selectively to find vegetation that is more nutritious with less fiber (Kufeld 1973). They will adjust to vegetation availability when other herbivores are present (Kufeld 1973) or when natural predators such as wolves are present (Beschta and Ripple 2009). Elk have similar diets to bison, but when bison are present, they tend to eat more forbs and browse if available while bison exploit grasses (Christianson and Creel 2007). Competitive browsing with white-tailed deer occurs during spring, summer, and winter (Sullivan 1988, Westfall 1989). Summer browse exploits grasses and sedges as they become available. Winter browse tends to consist more of shrubs such as snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*) and midstory trees such as maple species (*Acer* spp.) (Irby et al. 2000, Feldhamer et al. 2003, Wisdom et al. 2006). Weisberg et al. (2002) found that elk densities of 1.6 animals/km^2 caused a decrease of 23% in palatable shrub leaf biomass. Elk density at SHNGP is 2.9 animals/km^2 under the current management plan. Soil compaction by elk may affect understory vegetation, but no published studies to date have been reported to determine these effects. Therefore, elk are likely to have similar impacts to bison, but to a lesser extent given the size differences.

White-tailed Deer (*Odocoileus virginianus*): White-tailed deer were historically found in the riparian areas of the Great Plains (Fulbright and Ortega-Santos 2013). As European settlers moved into Great Plains states such as North Dakota, they hunted deer to near extirpation (Compton et al. 1988, Fulbright and Ortega-Santos 2013). Hunting regulations, agricultural plantings, and tree plantings for wind breaks allowed deer populations to return and exceed historical populations (Vercauteren and Hygnstrom 1998, Fulbright and Ortega-Santos 2013, NDGF 2014). Deer management now involves balancing high numbers that allow hunter satisfaction against crop depredation complaints from farmers. Deer use forest vegetation for cover and as a food source for browse at SHNGP and are a significant community member in shaping forest composition and structure (Russell et al. 2001, Kuiters and Slim 2002, Côté et al. 2004, Smith et al. 2007).

The diet of deer includes seeds, woody vegetation, forbs, and, to a lesser extent, grasses and sedges (DelGiudice et al. 2013). Deer have smaller rumens proportionally when compared to other ungulates and require higher quality forage. Deer chew their food to mix it with saliva and later regurgitate for additional grinding. This combination of digestive characteristics helps deer digest woody foods, but also requires the deer to be more selective in food choices. Thus, deer will choose the highest protein, lowest fiber parts of a plant for consumption (Feldhamer et al. 2003). Selective foraging can alter plant form, depress plant growth, and reduce seedling survival, and thus, with repeated browsing, kill tree saplings; all of these results are plant species dependent and deer do not affect all woody vegetation the same (Côté et al. 2004). Deer may also affect understory and midstory populations by decreasing plant fecundity (i.e. decreasing the proportion of reproductive structures that mature to yield fruit). There are many studies comparing vegetation with low and high deer densities that suggest deer have a significant

impact (Russell et al. 2001, Côté et al. 2004). Furthermore, deer have been shown to affect both the understory and the midstory to their browse line (Russell et al. 2001, Wisdom et al. 2006). However, low densities of deer or herbivores in general provide microhabitats for insect communities, seed germination, and plant growth through browsing as a disturbance. The threshold density for providing this ecosystem service versus negative impacts from overabundance is difficult to determine because it is site specific (Gill and Morgan 2009).

AVIAN ECOLOGY AT SHNGP

Although many avian species breed at SHNGP, our study focused on four woodland species, ovenbird (*Seiurus aurocapilla*), yellow warblers (*Dendroica petechia*), American redstart (*Setophaga ruticilla*), and red-eyed vireo (*Vireo olivaceus*) which represent the different layers of the forest structure they use. Therefore, each species represents a different canopy level and all are known to have breeding populations in the area. Further, these four birds are easy to recognize by their songs which makes them easy to locate and identify in avian surveys.

Ovenbird (*Seiurus aurocapilla*): The ovenbird winters in Central America and parts of the southeastern United States, but breeds in North America. These birds, as well as other migratory insectivores, time their migration and breeding to take advantage of large summer insect populations. The ovenbird nests on the ground and also forages primarily on the ground, but will opportunistically forage on outbreaks of insects such as spruce budworm (*Choristoneura fumiferana*) in the midstory. Nest success rates are considerably higher if large contiguous tracts of mature deciduous or mixed deciduous/coniferous forests with closed-canopies are used (Burke and Nol 2000, Kirk and Hobson 2001, Girard et al. 2004). The ovenbird prefers less ground cover, deeper leaf litter, higher biomass (Smith and Shugart 1987, Burke and Nol 1998, Seagle and Sturtevant 2005, Porneluzi et al. 2011), and canopy heights 16 – 22m with 60% - 90%

canopy closure (Porneluzi et al. 2011). A closed canopy holds in more moisture and increases the insect population (Porneluzi et al. 2011). In areas less than 100 hectares in size the ovenbird raises more brown headed cowbird young (*Molothrus ater*), a nest parasite found at habitat edges, resulting in less nestling success of their own young than in larger forest tracts (Morimoto et al. 2012). Ovenbirds also choose larger forests so that it has room to segregate itself from other warblers to avoid food competition (Porneluzi et al. 2011). Based on foraging and nesting characteristics, ovenbirds represent an understory species.

Yellow Warbler (*Setophaga petechia*): The yellow warbler is one of the most abundant and widespread Neotropical migrants whose breeding habitats can be found in most of North America, southern Canada and Alaska (Lowther et al. 1999). These warblers prefer shrubby habitats such as wet, deciduous thickets, disturbed areas, early successional with shrubby growth (Lowther et al. 1999), shrub uplands, old fields, semi-open wet deciduous forests (McPeek and Adams 1994), and human-influenced habitats which have thickets and hedgerows such as power lines, roadsides, farmland, and parks (Campbell et al. 2001). The yellow warbler winters in South America. Foraging behavior includes insect gleaning along small and large tree and shrub limbs from 0.3 – 16.8 m above ground and never on the ground (Frydendall 1969,Busby and Sealy 1979,Lowther et al. 1999). Some hawking behavior also has been documented (Kessel 1989). Breeding territories vary depending on habitat quality, but averaged 0.2 ha in Iowa (Kendeigh 1941) and 0.043 to 0.047 ha in Manitoba (Hobson and Sealy 1989). Males may defend two breeding territories with successful nesting in each (Ford 1996). The mating system of the yellow warbler is monogamous with seasonal pair bonding, but occasionally polygynous, with only one brood per season for females (Frydendall 1967, Lowther et al. 1999). Nest height varies with area but ranges 0-14 m with most at 1 – 2 m or high understory to low midstory

(Campbell et al. 2001). Yellow warblers are a commonly documented host to brown-headed cowbird nest parasitism due, in part, to habitat overlap (Lowther et al. 1999). The yellow warbler represents an understory to low midstory species based on foraging and nesting characteristics.

American redstart (*Setophaga ruticilla*): American Redstarts spend the majority of the year in the tropics, but they migrate north to breeding grounds in eastern North America and Canada (Sherry and Holmes 1997). The American Redstart prefers large tracts of deciduous habitat (>4,000 ha) with a shrubby midstory. Both male and females forage throughout the midstory and up to the top of canopy. They do not have specific insect preferences and will eat whatever insects are available on leaves, branches, and trunks. While molting at the end of the breeding season, the bird spends most of its time in dense vegetation in the midstory or canopy (Lovette and Holmes 1995). Nests are built between 1 – 8 meters above the ground against tree trunks. Due to nesting and foraging preferences of redstarts, they represent a species preferring the midstory and low canopy layers.

American Redstarts have delayed maturation, so it takes two years for the males to mature, making it difficult to sometimes discern breeding adult males (after second year) from subadults (second year). As second year males (second summer), they possess a female-like plumage, but sing mate attracting songs like adult males. If there are not enough adult males present in a breeding area, females will mate with these subadults (Sherry and Holmes 1997). In areas where there are enough adult males, it is thought that the subadult avoids aggressive displacement from an adult male's territory by plumage mimicry of female, but the juveniles may "sneak" copulation opportunities with the male's mate (Rohwer et al. 1980, Perreault et al. 1997, Hawkins et al. 2012).

Red-eyed vireo (*Vireo olivaceus*): Red-eyed vireos winter in South America and migrate to breeding grounds in the eastern half of North America, northern states bordering Canada, Canada, and Alaska (Cimprich et al. 2000). Red-eyed vireo can be found in both deciduous and mixed deciduous-coniferous forests of North America during the breeding season (Cimprich et al. 2000). This bird requires understory shrubs and is absent from areas without a midstory (Sutton 1949, James 1976). Red-eyed vireos prefer the forest interior over the edge and are often found by small openings in the forest canopy (Crawford et al. 1981). This species forages in the canopy and subcanopy (upper 1/3 of tree) along the branches picking insects off the leaves. Nests are built in midstory or low canopy (Cimprich et al. 2000). Based on these foraging and nesting characteristics, red-eyed vireo was chosen to represent subcanopy and canopy forest layers.

FOREST ECOLOGY

Forest structure and composition is important to understanding the animal species present in the community and how they utilize the forest habitat. SHNGP is characterized as a North Dakota deciduous forest (USFWS 2008, Haugen et al. 2012). There are many definitions for structural layers of forest; but we have chosen the following based on natural gradations. Understory or the ground cover layer up to 1.5 meters is made of woody and herbaceous vegetation and seedlings. The midstory layer, 1.5 – 7 meters from the ground, is comprised of shrubs and saplings, and the overstory or canopy layer, at or above 7 meters from the ground, contains mature trees. Uneven aged forests or forests with many different age classes promote biodiversity by having multiple vegetation layers. This stratified configuration creates structural diversity and fosters a range of niches for insect production, avian foraging and nesting, and cover for a variety of animals (MacArthur and MacArthur 1961, Lawton 1983, McCoy and Bell 1991, Tews et al. 2004).

A forest can either sustain itself with regeneration (seed germination and seedling recruitment and/or vegetative reproduction such as suckering) or enter another stage of succession with new species of trees replacing previous species (Barnes et al. 1997). Reproductive trees, shade tolerance, moisture and seed bed suitability are drivers of forest sustainability and succession (Barnes et al. 1997). Seed trees provide seed stock for germination or rhizomes for asexual reproduction.

Shade tolerance determines if a seedling can successfully grow under the canopy of an existing forest or requires an open canopy which allows sunlight to reach the forest floor. Canopy closure determines, in part, the amount of insects present which serves as a food source to birds and mammals (Porneluzi et al. 2011). Seed bed suitability requirements are determined by the tree species (e.g. bur oak (*Quercus macrocarpa*) acorns need to be in mineral soil with a light covering of duff) (Barnes et al. 1997, Johnson et al. 2009). Natural disturbances such as fire and tree fall (i.e., death and downing of a tree) create openings, which promote shade intolerant species. Fire and grazing also change the depth of litter layer which can determine which species of seed germinate. SHNGP is dependent on good management of all of these tools, fire, grazing/browsing, and natural tree fall or cutting to create openings in the canopy, to maintain species and structural diversity of the forest habitats.

STUDY OBJECTIVES AND HYPOTHESES

The specific aims of this study were to determine effects of decreasing ungulate density on forest regeneration in SHNGP, and concurrent effects on selected avian populations of the forest community. To achieve these goals we estimated regeneration and species richness of woody species in the forest understory compared to pre-herd reduction levels (Chapter 2). We surveyed four target species of birds and their response to vegetation in grazed treatment areas as

compared with reference areas lacking bison and elk (Chapter 3). At the onset of this project, we hypothesized the following scenarios for forest and bird responses to ungulates.

Objective I:

(1) Decreased numbers of browsers/grazers will result in increased tree seedling densities.

With less browsing pressure, there is opportunity for seedlings to survive and be recruited to the understory and midstory (Attiwill 1994, Peterson and Carson 1996, Bugalho et al. 2013).

(2) Decreased ungulate densities will result in increasing species richness in the forest understory.

With fewer ungulates, there is more selective browsing pressure, coupled with areas of disturbance caused by previously heavy browsing pressure. Selective browsing pressure allows less palatable species to survive and be recruited to the understory and midstory (Augustine 1998, Takahashi and Kaji 2001, Tremblay et al. 2005). If the number of ungulates is low enough, the preferred browse should also have seedlings escape browsing pressure and survive to recruitment into understory and midstory (Augustine 1998, Takahashi and Kaji 2001, Tremblay et al. 2005).

The previously heavily browsed areas have less understory and midstory competition for light, allowing more opportunity for pioneering species such as aspen or hazelnut to germinate or use vegetative reproduction to gain a foothold (Bork et al. 2013, Dreisilker et al. 2014). Understory recruitment of pioneering species is also dependent on canopy closure and the shade tolerance of species. Naturally occurring tree fall creates openings in the canopy allowing for shade intolerant species such as bur oak to germinate and grow (Runkle 1981, Canham et al. 1990, Lertzman et al. 1996, Busing and White 1997).

Objective 2:

(3) Song bird populations will change in abundance and species richness in response to changes in vegetative structure found across grazed and ungrazed areas.

With decreased ungulates, we predict increases in understory and midstory vegetation creating more nesting and foraging sites for bird species. Heavy browsing creates more homogenized landscapes allowing fewer niches for bird species (Stromayer and Warren 1997, Rooney 2009), therefore, causing lower densities and diversity of birds (McShea and Rappole 2000). Results from this study will be used to determine options for future management strategies of continued ungulate and forest management (Chapter 4).

STUDY APPROACHES

The combination of forested land with bison, elk, and white-tailed deer at SHNGP is unique in North Dakota. Only 2% of North Dakota is wooded and no other area has this combination of large herbivores. Further SHNGP has both upland hardwood and bottomland hardwood forests and areas with and without grazing, making it an ideal location for understanding multiple herbivore interactions with plant and bird communities.

Forest Regeneration and Species Richness: We define a forest as having sustainable regeneration and maximum species richness through recruitment to understory. To assess regeneration and species richness, we used forest inventory techniques that North Dakota Forestry used in the original surveys (Burns et al. 1990) so we could compare the 2012 vegetation to 2005 to determine changes as a result of herd reduction. To analyze regeneration through seedling germination and recruitment to understory, we used a negative binomial regression (Ver Hoef and Boveng 2007, Zuur et al. 2009). We modeled relationship of seedling density (response variable) to various predictor variables including year (2005, 2012), treatment

(grazed, ungrazed), and habitat type (upland, bottomland). Estimated variable relationships demonstrated an increased regeneration in grazed (treatment) areas, but level of regeneration still less than ungrazed (reference) areas (Chapter 2).

Species accumulation curves were used to examine woody species richness (Gotelli and Colwell 2001, Ellison and Gotelli 2013). The curves used woody stem count datasets for each habitat type to determine number of species present and to estimate maximum number of species likely (Chao et al. 2009). This allowed us to compare the grazed to ungrazed revealing a lack of species richness returning with the improved regeneration (Chapter 2).

Avian Abundance at SHNGP

To evaluate changes in bird abundance before and after herd reduction treatment, point counts of singing males were used. Point counts are a common method used to survey birds based upon song and visual identification (Fuller and Langslow 1984, Ralph et al. 1998, Johnson 2000). Baseline bird surveys conducted in 2004 at 25 woodland points provided a point of comparison for surveys conducted during this survey. Repeated point count surveys can be analyzed using Royle repeat count methods (Royle et al. 2005) to allow for estimation of abundance and detection relative to predictor variables such as grazing, habitat type, year and various vegetation metrics (Chapter 3).

Using information on both forest vegetation and avian responses allowed us to discuss community relationships among birds, forest vegetation, and ungulates that may influence management options. We propose future management options of ungulates that maintain the goals of healthy forest structure and diversity and healthy populations of migratory birds and indigenous wildlife.

LITERATURE CITED

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63:247-300.

Augustine, D. J. a. M., S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62: 1165-1183

Bailey, D. W., J. E. Gross, E. A. Laca, L. R. Rittenhouse, M. B. Coughenour, D. M. Swift, and P. L. Sims. 1996. Mechanisms that result in large herbivore grazing distribution patterns. Journal of Range Management 49:386-400.

Barnes, B. V., D. R. Zak, S. R. Denton, and S. H. Spurr. 1997. Forest Ecology. John Wiley and Sons, New York, USA

Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the Interior West. Conservation Biology 11:315-327.

Bertie, S., and R. Sweitzer. Unpublished. Carrying capacity for ungulates at Sullys Hill National Game Preserve. University of North Dakota, Grand Forks, North Dakota.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401-2414.

Bezkorowajnyj, P., A. Gordon, and R. McBride. 1993. The effect of cattle foot traffic on soil compaction in a silvo-pastoral system. Agroforestry Systems 21:1-10.

Bork, E. W., C. N. Carlyle, J. F. Cahill, R. E. Haddow, and R. J. Hudson. 2013. Disentangling herbivore impacts on *Populus tremuloides*: a comparison of native ungulates and cattle in Canada's Aspen Parkland. Oecologia 173:895-904.

Boyd, D. P. 2003. Conservation of North American bison: status and recommendations. Ph.D. Dissertation, University of Calgary, Alberta, Canada.

Bugalho, M. N., I. Ibáñez, and J. S. Clark. 2013. The effects of deer herbivory and forest type on tree recruitment vary with plant growth stage. Forest Ecology and Management 308:90-100.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. The Auk 115:96-104.

Burke, D. M., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecological Applications 10:1749-1761.

Busby, D. G., and S. G. Sealy. 1979. Feeding ecology of a population of nesting Yellow Warblers. Canadian Journal of Zoology 57:1670-1681.

Busing, R. T., and P. S. White. 1997. Species diversity and small-scale disturbance in an old-growth temperate forest: a consideration of gap partitioning concepts. Oikos 78:562-568.

Campbell, C., I. D. Campbell, C. B. Blyth, and J. H. McAndrews. 1994. Bison extirpation may have caused aspen expansion in western Canada. Ecography 17:360-362.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, A. C. Stewart, and M. C. McNall. 2001. The birds of British Columbia. Volume 4.British Columbia Museum, Victoria, British Columbia.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620-631.

Chao, A., R. K. Colwell, C. W. Lin, and N. J. Gotelli. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology 90:1125-1133.

Christianson, D. A., and S. Creel. 2007. A review of environmental factors affecting elk winter diets. The Journal of Wildlife Management 71:164-176.

Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle. 2000. Red-eyed vireo (*Vireo olivaceus*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 18 September 2012.

Collins, S. L., and G. E. Uno. 1983. The effect of early spring burning on vegetation in buffalo wallows. Bulletin of the Torrey Botanical Club 110:474-481.

Compton, B. B., R. J. Mackie, and G. L. Dusek. 1988. Factors influencing distribution of white-tailed deer in riparian habitats. The Journal of Wildlife Management 52:544-548.

Coppedge, B. R., and J. H. Shaw. 1997. Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. American Midland Naturalist 138:189-196.

Coppedge, B. R., D. M. Leslie Jr, and J. H. Shaw. 1998. Botanical composition of bison diets on tallgrass prairie in Oklahoma. Journal of Range Management 51:379-382.

Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 51:258-264.

Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113-147.

Crawford, H. S., R. G. Hooper, and R. W. Titterington. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. The Journal of Wildlife Management 45:680-692.

DelGiudice, G. D., B. A. Sampson, and J. H. Giudice. 2013. A long-term assessment of the effect of winter severity on the food habits of white-tailed deer. The Journal of Wildlife Management 77:1664-1675.

Dreisilker, K., A. Koeser, and J. O. Dawson. 2014. Enhancing establishment of white oak and American hazelnut enrichment plants in a mesic forest using understory removal and group selection. Ecological Restoration 32:171-178.

Ellison, G. N., and N. Gotelli. 2013. A primer of ecological statistics. Second edition. Sinauer, Sunderland, Massachusetts, USA.

Feldhamer, G. A., B. C. Thompson, and J. A. Chapman. 2003. Wild mammals of North America: biology, management, and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

Ferrero, A. 1991. Effect of compaction simulating cattle trampling on soil physical characteristics in woodland. Soil and Tillage Research 19:319-329.

Ford, N. L. 1996. Polyterritorial polygyny in north American passerines Journal of Field Ornithology 67:10-16.

Fortin, D., J. M. Fryxell, L. O'Brodovich, and D. Frandsen. 2003. Foraging ecology of bison at the landscape and plant community levels: the applicability of energy maximization principles. Oecologia 134:219-227.

Frydendall, M. J. 1967. Feeding ecology and territorial behavior of the yellow warbler. Dissertation. Utah State University, Logan, USA.

Frydendall, M. J. 1969. Feeding ecology and territorial behavior of the yellow warbler. Dissertation Abstracts International 29(7-B): 2679.

Fulbright, T. E., and J. A. Ortega-Santos. 2013. White-tailed deer habitat: ecology and management on rangelands. Texas A&M University Press, USA.

Fuller, R., and D. Langslow. 1984. Estimating numbers of birds by point counts: how long should counts last? Bird Study 31:195-202.

Gerlanc, N. M., and G. A. Kaufman. 2003. Use of bison wallows by anurans on Konza Prairie. The American Midland Naturalist 150:158-168.

Gill, R., and G. Morgan. 2009. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. Forestry 83:53-63.

Girard, C., M. Darveau, J. P. Savard, and J. Huot. 2004. Are temperate mixedwood forests perceived by birds as a distinct forest type? Canadian Journal of Forest Research 34:1895-1907.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379-391.

Hamza, M., and W. Anderson. 2005. Soil compaction in cropping systems: a review of the nature, causes and possible solutions. Soil and Tillage Research 82:121-145.

Harsel, R. 2005. Forest resource management plan for Sullys Hill National Game Preserve. North Dakota Forest Service, State of North Dakota, Lisbon, ND, USA.

Haugen, D. E., R. Harsel, A. Bergdahl, T. Claeys, C. W. Woodall, B. T. Wilson, S. J. Crocker, B. J. Butler, and C. M. Kurtz, Hatfield, M.A., Barnett, C.J., Domke, G.M., Kaisershot, D., Moser, W.K., Lister, A.J., Gormanson, D.D. 2012. North Dakota's Forests 2010. Newtown Square, PA, U.S.

Hawkins, G. L., G. E. Hill, and A. Mercadante. 2012. Delayed plumage maturation and delayed reproductive investment in birds. Biological Reviews 87:257-274.

Hobson, K. A., and S. G. Sealy. 1989. Female-female aggression in polygynously nesting yellow warblers. The Wilson Bulletin 101:84-86.

Irby, L. R., J. E. Norland, M. G. Sullivan, J. A. Westfall Jr, and P. Andersen. 2000. Dynamics of green ash woodlands in Theodore Roosevelt National Park. The Prairie Naturalist 32:77-102.

Isenberg, A. C. 2000. The destruction of the bison: an environmental history, 1750-1920. Cambridge University Press, New York, USA.

James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. The Wilson Bulletin 88:62-75.

Johnson, D. H. 2000. Point counts of birds: what are we estimating? Northern Prairie Wildlife Research Center, USA.

Johnson, P. S., S. R. Shifley, and R. Rogers. 2009. The ecology and silviculture of oaks. CABI Publishing New York, NY.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946-1957.

Keeley, J. E., and P. H. Zedler. 1998. Characterization and global distribution of vernal pools.

Kendeigh, S. C. 1941. Birds of a prairie community. Condor 43:165-174.

Kessel, B. 1989. Birds of the Seward Peninsula, Alaska: their biogeography, seasonality, and natural history. University of Alaska Press, Fairbanks, USA.

Kirk, D. A., and K. A. Hobson. 2001. Bird–habitat relationships in jack pine boreal forests. Forest Ecology and Management 147:217-243.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39-50.

Kohl, M. T., P. R. Krausman, K. Kunkel, and D. M. Williams. 2013. Bison versus cattle: are they ecologically synonymous? Rangeland Ecology and Management 66:721-731.

Kowalczyk, R., P. Taberlet, E. Coissac, A. Valentini, C. Miquel, T. Kamiński, and J. M. Wójcik. 2011. Influence of management practices on large herbivore diet—case of European bison in Białowieża Primeval Forest (Poland). Forest Ecology and Management 261:821-828.

Kufeld, R. C. 1973. Foods eaten by the Rocky Mountain elk. Journal of Range Management 26:106-113.

Kuiters, A., and P. Slim. 2002. Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biological Conservation 105:65-74.

Larter, N. C., and C. C. Gates. 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. Canadian Journal of Zoology 69:2677-2685.

Lawton, J. 1983. Plant architecture and the diversity of phytophagous insects. Annual review of Entomology 28:23-39.

Lertzman, K. P., G. D. Sutherland, A. Inselberg, and S. C. Saunders. 1996. Canopy gaps and the landscape mosaic in a coastal temperate rain forest. Ecology 77:1254-1270.

Lovette, I. J., and R. T. Holmes. 1995. Foraging behavior of American Redstarts in breeding and wintering habitats: implications for relative food availability. Condor 97:782-791.

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. 1999. Yellow warbler (*Setophaga petechia*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 19 September 2012.

MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594-598.

McCoy, E. D., and S. S. Bell. 1991. Habitat structure: the evolution and diversification of a complex topic. Pages 3-27 *in* S. S. Bell, E. D. McCoy, andH. R. Mushinsky, editors. Habitat structure. Springer, New York, USA.

McHugh, T. 1958. Social behavior of the American buffalo (*Bison bison bison*). Zoologica 43:1-40.

McMillan, B. R., K. A. Pfeiffer, and D. W. Kaufman. 2011. Vegetation responses to an animal-generated disturbance (bison wallows) in tallgrass prairie. The American Midland Naturalist 165:60-73.

McNaughton, S. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. Nature 345:613-615.

McPeek, G. A., and R. J. Adams. 1994. The birds of Michigan. Indiana University Press. Indianapolis, Indiana, USA.

McShea, W. J., and J. H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology 14:1161-1170.

Morimoto, D. C., M. A. Frankel, M. Hersek, and F. E. Wasserman. 2012. Forest fragmentation effects on ovenbird populations in the urban region of eastern Massachusetts, USA. Urban Habitats. http://urbanhabitats.org/v07n01/forestfragmentation_full.html. Accessed 20 October 2012.

NDGF. 2014. 2010-2014 Deer Population Information. http://gf.nd.gov/hunting/2010-2014-deer-population-information;.

Peden, D. G. 1976. Botanical composition of bison diets on shortgrass plains. American Midland Naturalist 96:225-229.

Perreault, S., R. E. Lemon, and U. Kuhnlein. 1997. Patterns and correlates of extrapair paternity in American redstarts (*Setophaga ruticilla*). Behavioral Ecology 8:612-621.

Peterson, C. J., and W. P. Carson. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. Canadian Journal of Forest Research 26:45-52.

Plumb, G. E., and J. L. Dodd. 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. Ecological Applications 3:631-643.

Polley, H. W., and S. L. Collins. 1984. Relationships of vegetation and environment in buffalo wallows. American Midland Naturalist 112:178-186.

Polley, H. W., and L. L. Wallace. 1986. The relationship of plant species heterogeneity to soil variation in buffalo wallows. The Southwestern Naturalist 31:493-501.

Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2011. Ovenbird (*Seiurus aurocapilla*), The Birds of North America Online *in* Ithaca: Cornell Lab of Ornithology, http://bna.birds.cornell.edu/bna/species/088. Accessed 21 September 2012.

Ralph, C. J., J. R. Sauer, and S. Droege. 1998. Monitoring bird populations by point counts. DIANE Publishing, Darby, Pennsylvania, USA.

Reynolds, H. W., R. M. Hansen, and D. G. Peden. 1978. Diets of the Slave River lowland bison herd, Northwest Territories, Canada. The Journal of Wildlife Management 42:581-590.

Rohwer, S., S. D. Fretwell, and D. M. Niles. 1980. Delayed maturation in passerine plumages and the deceptive acquisition of resources. American Naturalist 115:400-437.

Rooney, T. P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology 202:103-111.

Royle, J. A., J. D. Nichols, and M. Kéry. 2005. Modelling occurrence and abundance of species when detection is imperfect. Oikos 110:353-359.

Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. Ecology 62:1041-1051.

Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. The American Midland Naturalist 146:1-26.

Seabloom, R. 2011. The mammals of North Dakota. Institute for Regional Studies, North Dakota State University, Fargo, North Dakota, USA.

Seagle, S. W., and B. R. Sturtevant. 2005. Forest productivity predicts invertebrate biomass and ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian landscapes. Ecology 86:1531-1539.

Sherry, T. W., and R. T. Holmes. 1997. American redstart (*Setophaga ruticilla*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 20 September 2012.

Smith, B. L. 2013. Elk winter feeding = disease facilitation. The threat as CSW approaches wester feedgrounds. The Wildlife Society News. Online. http://news.wildlife.org/twp/2013-winter/elk-winter-feeding-disease-facilitation. Accessed 12 September 2014.

Smith, J. R., R. A. Sweitzer, and W. F. Jensen. 2007. Diets, movements, and consequences of providing wildlife food plots for white-tailed deer in central North Dakota. The Journal of Wildlife Management 71:2719-2726.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology 68:695-704.

Stromayer, K. A., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25:227-234.

Sullivan, M. G. 1988. Distribution, movements, habitat usage, food habits, and associated behavior of reintroduced elk in Theodore Roosevelt National Park. Thesis. Montana State University, Bozeman, USA.

Sutton, G. M. 1949. Studies of the nesting birds of the Edwin S. George Reserve, Part I: The Vireos. University of Michigan Press, Ann Arbor, Michigan, USA.

Takahashi, H., and K. Kaji. 2001. Fallen leaves and unpalatable plants as alternative foods for sika deer under food limitation. Ecological Research 16:257-262.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79-92.

Tremblay, J. P., I. Thibault, C. Dussault, J. Huot, and S. D. Côté. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. Canadian Journal of Zoology 83:1087-1096.

USFWS. 2008. Sullys Hill National Game Preserve: Comprehensive Conservation Plan (CCP 2008).

Veikley, L. R. 1984. Fenced Animal Management Plan. Devils Lake, ND: U.S. Department of the Interior, U.S. Fish and Wildlife Service, Devils Lake Wetland Management District.

Ver Hoef, J. M., and P. L. Boveng. 2007. Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? Ecology 88:2766-2772.

Vercauteren, K. C., and S. E. Hygnstrom. 1998. Effects of agricultural activities and hunting on home ranges of female white-tailed deer. The Journal of Wildlife Management 62:280-285.

Weisberg, P. J., N. Thompson Hobbs, J. E. Ellis, and M. B. Coughenour. 2002. An ecosystem approach to population management of ungulates. Journal of environmental management 65:181-197.

Westfall, J. A. 1989. The ecology of reintroduced elk in Theodore Roosevelt National Park, North Dakota. Dissertation, Montana State University, Bozeman, USA.

Whalley, W. R., E. Dumitru, and A. R. Dexter. 1995. Biological effects of soil compaction. Soil and Tillage Research 35:53-68.

Wisdom, M. J., Vavra, M. Boyd, J.M.,Hemstrom, M.A.,Ager, A.A. and B. K. Johnson. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Wildlife Society Bulletin 34:283-292.

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York, USA.

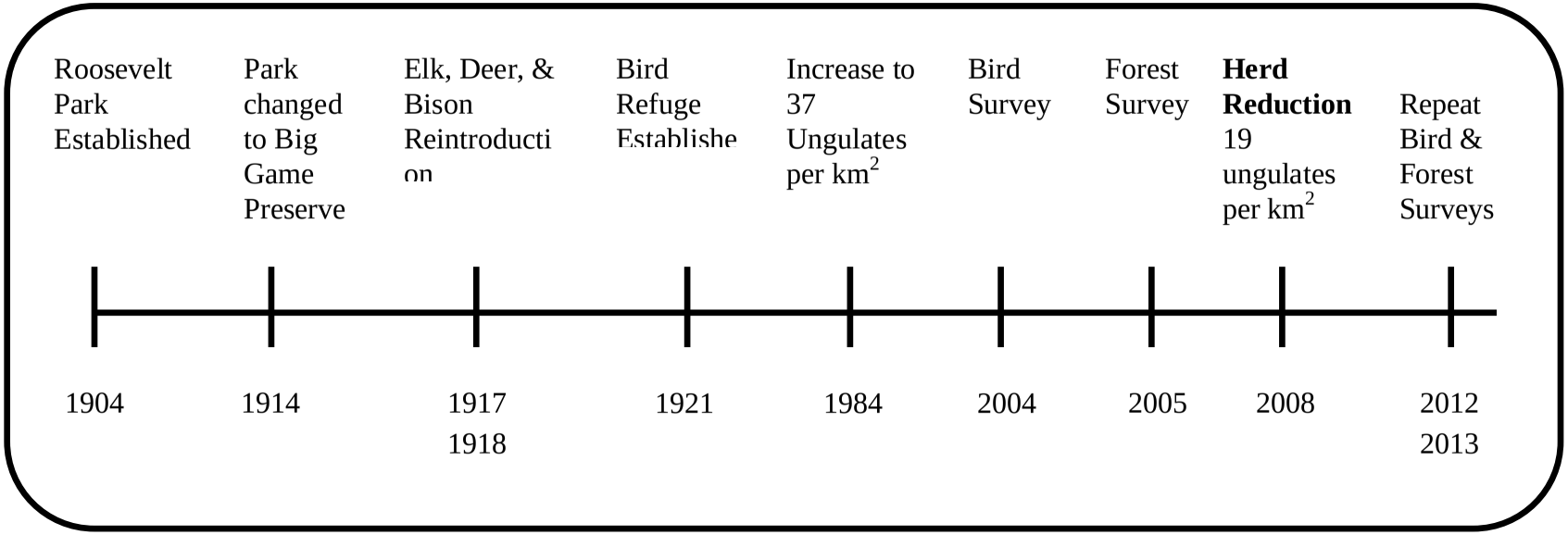


Figure 1. Timeline of major monitoring and management events of Sullys Hill National Game Preserve.

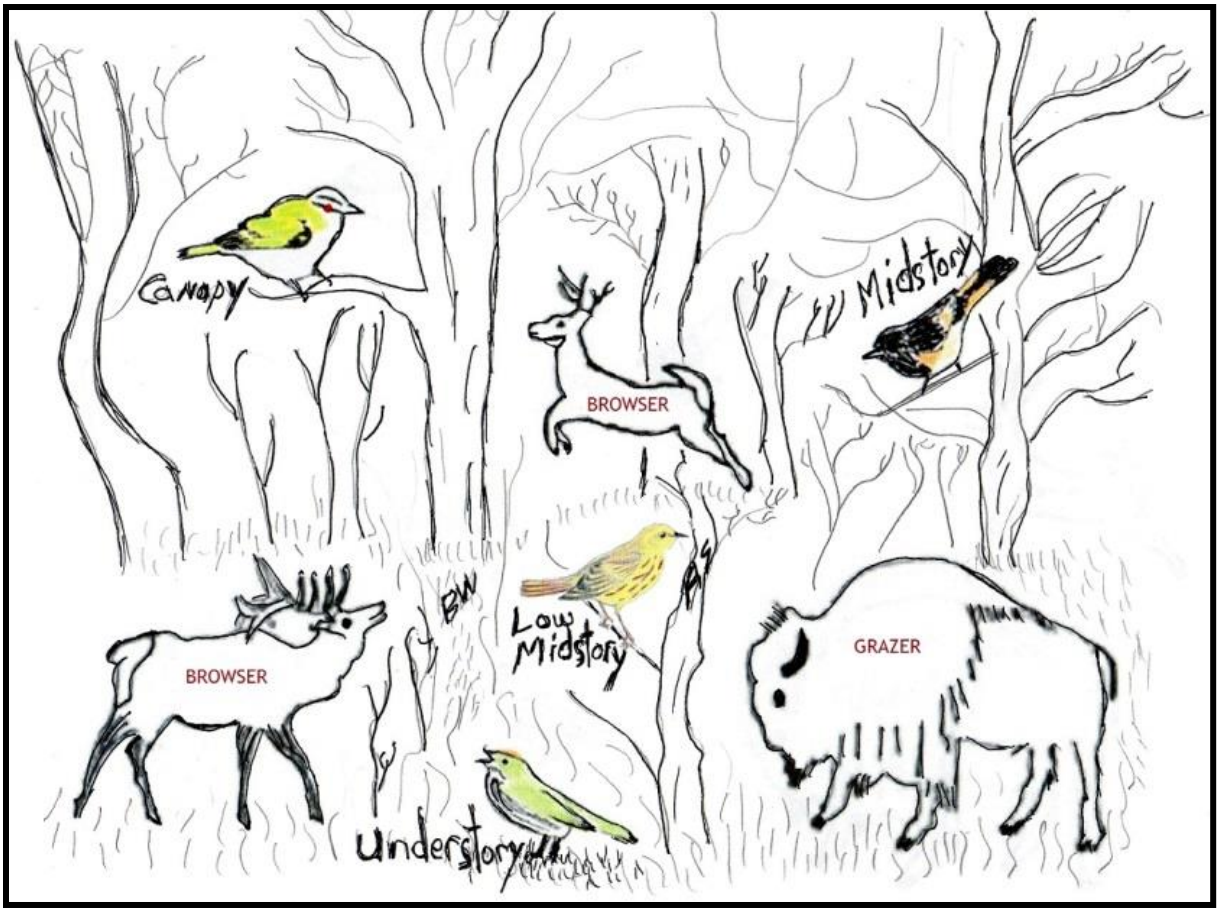


Figure 2: Plant – animal interactions. Deer and elk browse on understory and midstory. Bison graze on understory and affect midstory by horning and rubbing vegetation. All three ungulates affect nesting and foraging vegetation. Red-eyed vireos (top left) nest and forage in midstory and canopy. American redstarts (upper right) nest and forage in upper midstory. Yellow warbler (middle) nest and forage in low midstory. Ovenbird (bottom middle) nest and forage in understory.

CHAPTER II
FOREST REGENERATION RESPONSE TO MIXED UNGULATE REDUCTION AT SULLYS HILL NATIONAL GAME PRESERVE, A TEMPERATE DECIDUOUS FOREST: IS SEEDLING RECRUITMENT WITHOUT RETURN OF SPECIES RICHNESS ENOUGH?

ABSTRACT

Overexploitation of vegetation by white-tailed deer *(Odocoileus virginianus*) has been well documented, but determining effects of multiple large herbivores such as Rocky Mountain elk (*Cervus elaphus*), Plains bison (*Bison bison*), and white-tailed deer is much less understood. After 67 years of ungulate densities between 19 - 37 ungulates/km^2 (23 AUM/km^2), a forest survey conducted in 2005 at Sullys Hill National Game Preserve showed little to no forest regeneration. Herd sizes of all three ungulates were reduced from 37 ungulates/km^2 and maintained at approximately 19 ungulates/km^2 (11 AUM/5km^2) from 2008 to 2012. The objectives of our study were to determine if: 1) herd reduction successfully improved forest regeneration (i.e. sustainable germination and recruitment of tree seedlings), and 2) diversity of woody vegetation returned as compared to reference areas. Seventy random points were surveyed by counting and determining species of woody stems in a 4.0 m^2 (1/1000 acre) plot. We evaluated regeneration using negative binomial regression, and plant species diversity using species accumulation curves. We found improved regeneration in grazed/browsed areas post-herd reduction. Individual based species accumulation curves showed lower woody species diversity in grazed versus reference areas. Our findings suggest that lower densities of ungulates allowed for improved regeneration, but not a return of species richness over the herd reduction era.

INTRODUCTION

Effects of overabundant white-tailed deer *(Odocoileus virginianus*) populations have been well documented in short and long term studies (Horsley et al. 2003, Rooney and Waller 2003, Côté et al. 2004), but impacts from combinations of large herbivores are poorly understood. Sullys Hill National Game preserve (SHNGP) has re-introduced populations of Rocky Mountain Elk (*Cervus elaphus*), Plains Bison (*Bison bison*), and white-tailed deer (hereafter elk, bison, and deer, respectively). Long term overbrowsing by elk, bison, and deer is the suspected cause for changes in the deciduous forest structure of SHNGP.

Overbrowsing and overgrazing occurs when the number of ungulates exceeds the carrying capacity supported by vegetation. Studies demonstrating negative browsing impacts include a range of deer densities from 4 deer/km^2 (0.6 AUM/km^2; (Horsley et al. 2003) to 93 deer/km^2 (14.0 AUM/ km^2; (Abrams and Johnson 2012). The direct effects of deer and/or elk are due to selective browsing and subsequent responses of plant communities (Augustine 1998, Horsley et al. 2003, Côté et al. 2004). These effects include decreased tree regeneration (Gill 1992, Bellingham and Allan 2003, Rooney and Waller 2003, Didion et al. 2009, Taylor and Arends 2011, Roberts et al. 2014), altered understory and midstory woody and herbaceous plant composition (Augustine et al. 1998, Collard et al. 2010b, Abrams and Johnson 2012, Bugalho et al. 2013), and altered canopy structure and composition (Nuttle et al. 2011). Indirect effects result from altered plant communities (Rooney 2009).When combined with changes in nutrient cycling (Hobbs 1996), this can alter other animal communities in the ecosystem such as diversity of birds (DeCalesta 1994, Chollet et al. 2013), soil invertebrates (Whalley et al. 1995) or vegetation invertebrate communities (Allombert et al. 2005, J. Teichman et al. 2013). Ungulate choices can cause compositional increasers (i.e., browse tolerant or avoided species), decreasers

(i.e., browse favored species) (Horsley et al. 2003, Gill and Morgan 2009) and include the spread of invasive species (Baiser et al. 2008, Knight et al. 2009). Changes in vegetative composition and localized extirpations of herbaceous species (Augustine et al. 1998) can cause cascading effects that change soil, mycorrhiza fungi, densities of small mammals (Parsons et al. 2013, Shelton et al. 2014), amphibians (Brooks 1999), and reptiles (Greenwald et al. 2008). Further, insect predator – herbivore dynamics are determined, in part, by complexity of canopies. These complex canopies are created by trees and shrubs of multiple ages with intact branches, and this complexity can be lost with overbrowsing (Šipoš and Kindlmann 2013).

Potential impacts of megaherbivores such as bison and elk not only include over-browsing (Irby et al. 2000, Feldhamer et al. 2003, Wisdom et al. 2006), but also rubbing and horning which destroys midstory patches of seedlings and shrubs (Coppedge and Shaw 1997), and can alter topsoil properties by hoof impaction and wallowing (Bezkorowajnyj et al. 1993, Whalley et al. 1995, Belsky and Blumenthal 1997). All of these impacts can alter the health of a forest and its ability to regenerate or drive the forest to alternate stable states which may be less beneficial due to homogenization of vegetation (Stromayer and Warren 1997, Newman et al. 2014).

The goal of this study was to evaluate forest regeneration and species diversity after a 50% reduction in a multi-species ungulate herd (i.e., elk, bison, and deer) at SHNGP. This semi-free ranging herd is managed by the U.S. Fish and Wildlife Service within a 324 ha fenced enclosure. In 1917, seventeen elk and four deer were reintroduced to the preserve and six bison were added in 1918. All three herds increased to approximately eighteen animals/ herd by the early 1940's. From the 1940s to late 1980s, a minimum density of 19 ungulates/km^2 (11 AUM/km^2) was maintained (Figure 3). In 1984, a new ungulate management plan (Veikley

1984) allowed an increase to 40 animals/herd or 37 ungulates/km^2 (23 AUM/km^2; Table 2). Supplementary winter feeding of hay and grain was provided to reduce the impacts of ungulates on forest vegetation as of 1958 (Kowalczyk et al. 2011). In 2005 at the request of USFWS, the North Dakota Forest Service (NDFS) conducted a forest survey that revealed little regeneration was occurring, and overbrowsing by ungulates was the suspected cause. A new plan was implemented in 2008 that included culling approximately 50% of all three herds and adding a 10.1 ha exclosure (USFWS 2008). Specific management objectives in the plan for regeneration included ≥ 200 bur oak seedlings per hectare in uplands and ≥ 400 green ash seedlings per hectare, ≥ 80 American elm seedlings per hectare, and ≥ 200 basswood seedlings per hectare in the bottomlands at SHNGP (USFWS 2008). Therefore, the combined effects of a multi-species ungulate herd at densities between 19 – 37 ungulates/km^2 (11 – 23 AUMs/km^2) for seventy years allowed us to examine the effects of chronic over-browsing by comparing forest surveys before and after herd reductions at SHNGP.

METHODS

Study Area: SHNGP is located on the south side of Devils Lake in central North Dakota (centroid 502140, 5315194 UTM) with an average annual rainfall of 519 mm (CR 2014). It is a 675.8 ha refuge comprised of two units, a north block and a south block (Figure 4). The 324 hectare enclosure for bison, elk, and deer includes 166 ha of upland/bottomland forests, 145 ha lacustrine wetlands, and 12 ha native prairie. The ungrazed/unbrowsed reference sites have a population of deer that has not been formally surveyed. We were specifically interested in impacts on woody vegetation or browsing, but follow conventional rangeland vocabulary by referring to study areas as grazed or ungrazed, meaning inside the animal enclosure or outside the enclosure. Surveyed areas were divided into to two habitat types based on the initial forest

inventory: 1) upland hardwood, dominant species include bur oak (see Table 3 for scientific names of plants) and green ash; 2) bottomland hardwood, dominant species include basswood and green ash. These two habitat types were further divided based on grazing treatment, creating four groups: 1) upland hardwood grazed (UHG) 114 ha, 2) upland hardwood ungrazed (UHUG) 27 ha, 3) bottomland hardwood grazed (BHG) 52 ha, and 4) bottomland hardwood ungrazed (BHUG) 55 ha. Both ungrazed areas will serve as reference sites for comparison. Further, a 10.1 hectare area was fenced (hereafter referred to as exclosure) within the original fenced area at the time of the herd reduction. The exclosure provided a recovery reference area since it was originally grazed.

Field Methods: Across the north and south woodland blocks, 70 random points were selected by the NDFS proportionally to the four different habitat-grazing areas in the 2005. The original 70 forest survey points were recorded manually on maps. In 2012 GPS points were approximated according to maps supplied by the NDFS to conduct replicate surveys. At these points, understory vegetation was measured by counting all woody stems (seedlings < 5 cm DBH) and identifying them to species within a 1.13 m radius (1/1000 acre) of each survey point center (Burns and Honkala 1990, NDFS 1994). Sampling of the understory was conducted between 28 July and 18 August in 2005 and 7 July and 20 August in 2012.

Data Analysis: We defined *regeneration* as seedling germination and *recruitment* as a rate that allows the continued existence of a forest habitat. To evaluate the status of regeneration, we used stem count/ha and summary statistics to compare 2005 to 2012 and grazed to reference area for each habitat type from all 70 survey points. Summary statistics were calculated in program R version 3.0.1 (R Core 2013). Stem counts were used in subsequent regression analysis.

In order to determine the most appropriate regression for our stem density counts, we used a diagnostic test described in Ver Hoef and Bovent (2007) to determine if quasi-Poisson or negative binomial regression fit our data. The raw data was binned (bin size 500 stems/ha, 16 bins for 2005 dataset; bin size 1000 stems/ha, 50 bins for 2012 dataset). We then plotted $(Y_i - \mu_i)^2$ against μ_i, where Y = number of trials (observations), $\mu_i = \frac{successes}{\frac{1}{bins}}$, and a success as an occurrence. The plot was nonlinear supporting the use of a negative binomial regression (Ver Hoef and Boveng 2007).

We conducted a negative binomial regression using program SAS (Version 9.3, SAS Institute, Cary, NC) to evaluate the relationship between stem density and predictor variables. We hypothesized that stem density would increase in grazed habitats in 2012 relative to 2005 pre-herd reduction stem densities. Therefore, predictor variables of year (2005, 2012), treatment (grazed, ungrazed), and habitat type (upland, bottomland) were modeled using binary dummy variables. Baseline variables for the categorical covariates were 2005, ungrazed, and upland habitat type, compared to 2012, grazed, and bottomland respectively.

Candidate models were built using individual covariates and included additive and interactive combinations. Weighted Akaike's Information Criterion corrected for small sample sizes (AICc) from SAS were calculated and used to evaluate models to determine the simplest combination of predictors that best explained stem density (Burnham and Anderson 2002). Model-averaged estimates were calculated from the top 95% of models for covariates explaining stem density (Burnham and Anderson 2002, Anderson 2008).

We hypothesized that species richness would increase in the grazed areas in 2012 relative to 2005. To estimate species richness, species accumulation curves were plotted (Ellison and

Gotelli 2013). The number of survey points varied due to proportional sampling in each habitat type, and thus required a standardized sampling area. Since ten was the largest number of points common to all habitats, we chose ten random points from each habitat type in the dataset available for a standardized sampling area. We corrected for sampling effort using individual-based rarefaction (Gotelli and Ellison 2004) using program R. Species accumulation curves were estimated separately for upland and bottomland habitats based on rarefied datasets. Upland hardwood ungrazed 2012 (UHUG 2012) and bottomland hardwood ungrazed 2012 (BHUG 2012) were used as the reference states for each dataset. Asymptotic estimation or estimation of the maximum number of species was calculated using Chao equations (Chao et al. 2009). The equations are based on the presence of singletons (i.e., species in the sample represented by one individual) and doubletons (i.e., species in the sample represented by two individuals). If singletons are present in a sample, it indicates that there may still be rare species missed in the counts. Chao estimates were also included to determine if enough individuals were observed or how many more would be needed to reach maximum species richness.

RESULTS

Regeneration: Average tree seedling/ha between 2005 to 2012 showed increasing trends of stem density, but substantial variation in some years across the habitat-treatment combinations (Table 4). UHG had no regeneration from seedlings in 2005, but an average of 70 seedlings/ha in 2012 surveys (Table 4). These sites were dominated by bur oak. UHUG averaged between 118 and 263 seedlings/ha in 2005 and 2012, respectively. UHUG sites were dominated by basswood and green ash in 2005, but more evenly distributed between bur oak and green ash in 2012 surveys. Further, one large stand of ironwood was found in 2012, but not observed in 2005. BHG averaged 55 tree seedlings/ha in 2005 and 99 seedlings/ha in 2012. These areas were dominated

by basswood in 2005, but more evenly distributed between basswood, boxelder and bur oak in 2012. BHUG averaged 204 and 250 seedlings/ha in 2005 and 2012 respectively. BHUG sites were dominated by bur oak and green ash in 2005 and basswood in 2012. The created exclosure formerly a part of the UHG sites, had no seedling regeneration when surveyed in 2012.

Shrub stems/ha also demonstrated increasing trends with substantial variability between 2005 and 2012. The largest shrub densities were observed in the grazed areas during the 2012 surveys (Table 5). All habitat types and years were dominated by chokecherry and snowberry except the BHUG sites. This area had more species diversity and included hazelnut which was not found in grazed areas (Table 5).

Eleven candidate models were constructed to evaluate stem density of tree species as a response variable and habitat, treatment, and year as explanatory variables (Table 20). The best model based on weighted AICc was an additive model including treatment, year, and habitat. This model is 1.5 and 3.0 times more likely than the second and third best models, respectively (Table 6). The top three models carried 96% of weighted AICc scores and were used to calculate model-averaged parameter estimates (Table 7). Model-averaged estimates for treatment did not have 95% confidence intervals overlapping zero, indicating that when comparing ungrazed (baseline) to grazed habitats and holding year and habitat type constant, the difference would on average decrease by 16.4 stems/ha (or a difference in the logs of 2.8) . The variable year was in the top two models. From 2005 to 2012, stem density increased on average by 7.2 stems/ha across SHNGP. Confidence intervals encompassing 0 indicated that the habitat type estimates are not precise enough to conclusively detect the direction of a relationship between stem density and habitat type. Although treatment and year suggest an effect on stem density, examination of

the deviance from the null model suggests very little variation has been accounted for using these predictor variables.

Species Richness: Species accumulation curves for UHG indicated that species richness of UHG for both 2005 and 2012 was lower than the 95% CI of UHUG 2012, the reference site (Figure 5). The species accumulation curves for bottomland habitat were similar (Figure 6).

Using Chao estimators (Chao et al. 2009), we found asymptotes or the estimate of the maximum number of species was reached in several of the habitat types (Table 8). Grazed habitats within all of the 2012 surveys reached the estimated maximum number of species, indicating that addition of more sampling sites is unlikely to increase species richness.

DISCUSSION

Our results suggest an increase in regeneration in the grazed areas at SHNGP and support the hypothesis that fewer ungulates have allowed a return of tree seedlings. However, the rate of seedling germination and recruitment to seedling status is still lower than the ungrazed reference sites or the target numbers listed in the objectives of SHNGP Comprehensive Conservation Plan (USFWS 2008).

Our results represent only a short temporal (4 year) scale for evaluating changes in regeneration, but these results agree with other studies indicating the start of recovery of understory species. For example recovery may not be observed until as late as 14 years post herd reduction (Collard et al. 2010b, Price et al. 2010). Tanentzap et al. (2012) proposed several reasons for slow recovery, including: 1) slow growth rate of plants relative to the amount of biomass consumed by herbivores (i.e., ungulate density is still too high); 2) depletion of seed sources for preferred browse plants; 3) formation of alternate vegetation types under high browsing pressure; 4) preferential browsing of forage even under low densities; 5) variation in

browse damage of preferred species dependent on plant community composition; 6) suppression of trophic cascades; and 7) changes in abiotic conditions associated with other ecological processes.

Natural regeneration in hardwood forests relies on seed germination and recruitment and vegetative reproduction (Attiwill 1994, Peterson and Carson 1996). This requires adult trees as seed sources since few hardwood seeds remain viable in seed banks (Hyatt and Casper 2000). Depletion of seed sources for preferred browse plants may have multiple causes (Tanentzap et al. 2012). Deciduous forest tree species produce large amounts of seed (e.g., acorn mast that serves as a food source for several animals and is dependent on bird and animal dispersal (Bjorkbom et al. 1965, Marquis et al. 1976, Horsley and Marquis 1983, Bonner 2008). Seeds from species such as bur oak, green ash, and basswood do not remain viable more than a year in a seed bank (Marquis 1975, Thompson 1987, Nathan and Muller-Landau 2000). In addition to a lack of seed germination, a lack of vegetative reproduction is also present. Hazelnut species (both *Corylus americana* and *C. cornuta*) are present in upland and bottomland ungrazed areas outside of, but within a meter of the enclosure, yet none are observed within the ungulate enclosure. Hazelnut spreads by vegetative propagation and is seen in early and mid-successional phases (Whitford 1949), so we would expect to see a return with fewer browsers. Further, hazelnut was not found in the exclosure which has been resting from browsing and grazing pressure for four years.

Formation of alternate vegetation types under high browsing pressure may be due to plant-plant interactions such as competition or higher order interactions (Billick and Case 1994). Survey personnel observed unnaturally large patches of sarsaparilla that may out-compete seedlings or vegetation structures for resources such as sunlight. There were few small forbs or sedges underneath the umbrella of sarsaparilla, and patches as large as 0.5 ha appeared as a

monoculture. Early spring emergence and umbrella like structure may allow sarsaparilla to act as an ecological filter, inhibiting seed germination or stunting vegetative propagule success in a manner similar to ferns (George and Bazzaz 1999, De La Cretaz and Kelty 2002).

Long term preferential browsing of forage even under low ungulate densities may also be responsible for the apparent suppression of seedlings (Tanentzap et al. 2012). If considering just elk and deer, densities of 12 browsers/km^2 (5 AUM/ha) have been present for >60 years. This is above the negative impact threshold of 8 deer/km^2 (1.2 AUM/km^2) as found by Horsley et al. (2003), but they also note that thresholds are area dependent. Both elk and deer browse high nutrient parts of plants which are responsible for growth and/or reproductive structures. By browsing these down, they allow competitors such as sarsaparilla to flourish causing changes in understory plant composition. At higher densities, deer may supplement their diet with less preferred plants and after densities are lowered, deer browse on preferred plants continuing to suppress regeneration (Takahashi and Kaji 2001, Tremblay et al. 2005).

Further, within the enclosure there are no natural predators for bison, elk, and deer. The loss of trophic cascades may contribute to slow recovery of woody species because ungulate densities and use of resources are influenced by predators (Beschta and Ripple 2009, Ripple et al. 2010, Tanentzap et al. 2012). Low density of ungulates as a result of increased pressure from predators allows vegetation relief from browsing and increased regeneration (Ripple and Beschta 2007, Laundré et al. 2010, Terborgh and Estes 2010, Beschta and Ripple 2014).

Changes in abiotic conditions associated with other ecological processes may be present and are restricting regeneration. Natural regeneration requires disturbance such as fire or tree fall for seed germination and recruitment because of effects on seedbed conditions and space to grow and receive sunlight (e.g. fire removes duff exposing mineral soil which is a required substrate

for some species (Schaetzl et al. 1988, Baskin and Baskin 2001). Although fire has been used as a tool at SHNGP, burn history is not well documented. However, these periodic disturbances in the future may facilitate germination and recruitment in this system.

Research on ungulate impacts to regeneration are primarily based on single *Cervidae* studies and may not address additional interactions from a second browser, elk, and a grazer, bison. Bison graze graminoids, allowing an increase in forbs and woody vegetation (Coppedge and Shaw 1998). Elk and deer, however, graze fewer forbs and graminoids and browse woody vegetation allowing an increase in some forbs and graminoids (Rooney 2009). The presence of all three ungulates means that there is browsing/grazing pressure on a broader spectrum of plants allowing a variety of plant-plant and plant-herbivore interactions to occur that have not been previously studied in the literature.

We observed a substantial amount of variation in stem density and variance in the ungrazed areas between 2005 and 2012 than in the grazed areas (Figure 7). Given this study had one site, SHNGP, and no true spatial replication; it is difficult to account for some of the variation. It is also difficult to find comparable sites with similar ungulates herds (Bachand et al. 2014). Much of the stem density variation may be the result of these complex interactions not described with the explanatory variables we measured. Observer or climate effects may have provided additional variation, but if they are playing a large role, this would be confounded with year. Other potential factors include interactions between the seed bank and disturbances such as prescribed fire. Burns were conducted on SHNGP, and, although burn records are not available, long-term staff are unaware of any historical burns in the BHUG sites located in the southern block of the refuge. Interestingly, BHUG sites have the highest species diversity. Finally, although elk and bison herds are managed more closely, white-tailed deer are able to cross cattle

guards and it is more difficult to monitor their populations seasonally. This is complicated by ungrazed reference sites without monitoring of deer populations. As a result, some of the variation in stem density may be effects of oscillating deer populations across the study area. It is thought, however, that beginning in 2010, deer populations in the enclosure were below the target of ≤ 18 deer. This trend also was observed in the prairie habitats across much of North Dakota (personal communication, Mark Fisher, SHNGP biologist, USFWS).

Species accumulation curves for both upland hardwood and bottomland habitats indicated that species richness was lower in the grazed areas than ungrazed areas, in spite of improved regeneration. The grazed area curves were lower and outside the 95% CI of ungrazed reference sites. The grazed area curves and exclosure curve also leveled off at or close to the asymptote or maximum species number. Thus, our sampling effort likely was sufficient to detect even rare species that may have been missed, providing evidence of reduced species richness between the grazed and ungrazed sites. Longer term deer studies support these findings and demonstrate long term browsing as a direct or indirect cause of prolonged loss of tree diversity and local extirpations of woody and herbaceous species (Horsley et al. 2003, Rooney and Waller 2003, Nuttle et al. 2011, White 2012). Although only a few long term studies of mixed ungulate overbrowsing exist in the literature, these studies also support loss of forest structure and species diversity (Singer and Norland 1994, Brookshire et al. 2002, Ripple et al. 2010).

Of considerable importance is the lack of regeneration in the exclosure. This area was browsed since 1918, but was fenced off in 2008 and allowed to rest from all ungulates for four years prior to repeated surveys. Our results are consistent with other exclosure studies (Collard et al. 2010a, Goetsch et al. 2011, Abrams and Johnson 2012) in that it has a homogenized understory and midstory consisting of chokecherry and snowberry, but the lack of disturbance

by storm, fire, or mesoherbivores may explain the low species diversity in area. Further work on disturbance in long-term exclosure areas needs to be conducted to clarify the cause of low species diversity.

Results from long term browsing by ungulates indicate the need to monitor vegetation composition as well as ungulate composition. A density of 19 bison, elk, and deer /km^2 (11 AUMs/km^2) is a lower density of ungulates than other studies that documented long-term damage to woody species regeneration, density, and diversity (Horsley et al. 2003). Low densities of herbivores are considered beneficial to forest areas because they promote diversity of vegetation and create localized microhabitats for insects or seedling germination through selective browsing (Russell et al. 2001, Royo et al. 2010). It is not clear how small a mixed ungulate density should be to promote healthy reforestation. Gill and Morgan (2009) offer $\geq$ 14 deer/km^2 (2.1 AUMs/km^2) as a threshold for negative browsing effects, but acknowledge that a threshold is dependent on specific ecosystem characteristics and the ungulates present.

Supplemental feeding is currently used as a management tool. This tool allows recruitment of seedlings into the understory and midstory by diverting winter browsing pressure to the supplemental feed. Without continued use of this tool, bison increase browsing by as much as 65% and favor *Carpinus/Corylus* species. *Corylus* is a midstory species missing from within, but present outside of the enclosure (Kowalczyk et al. 2011).

This study is reviewing only two years of data (2004, 2012) with predictor variables that do not explain much variation as noted by comparing model deviance to null deviance. Some of the confounding factors such as increased variability in stem counts may be due to the complexity of the system. There are both interspecific interactions between three ungulate species and woody vegetation as well as intraspecific interactions among the ungulates and

higher order interactions among vegetation. Including all three game species in the study is unique, but provides limited inference because there are no other replicate sites within the state. Analysis of vegetation before-after herd reduction has revealed small changes over a short temporal span and indicates the need for a longer time scale and the inclusion of more predictor variables such as growing season precipitation and precipitation from snowfall.

MANAGEMENT IMPLICATIONS

Management options available to meet the seedling germination and recruitment objectives include time, disturbance, potentially increased culling, and increased supplemental feeding. Enough time, however, may not have elapsed to document the desired changes in seedling recruitment and diversity given some studies suggest it may take >14 years to observe responses to changing ungulate densities (Collard et al. 2010b, Price et al. 2010).

Forest recovery scenarios discussed in the SHNGP Comprehensive Conservation Plan (USFWS 2008:45) include alternate ungulate density scenarios: 15 elk, 5 deer, and 19 bison, or a decrease in the number of browsers. This scenario was proposed based upon continued supplementary feeding. If supplementary feeding is discontinued, SHNGP might support this ungulate density, but the animals will be more dependent on browse and potentially have greater impacts on regeneration and woody diversity (Kowalczyk et al. 2011). Further, this scenario represents an opportunity to explore the differential feeding pressures of these ungulates. Continued disturbances from elk and deer will help prevent homogenization of plant communities to occur (Goetsch et al. 2011, Nuttle et al. 2011, Newman et al. 2014). Some browsers/grazers are needed to cause localized disturbance which leads to increased species richness (Boulanger et al. 2009). Changing the density of browsers to mimic cyclic populations decreases the severity of compositional shifts in vegetation as compared to steady browsing

pressure (Kuiters and Slim 2002, Didion et al. 2009). For example, reducing elk to "starter" herd sizes of 1-2 elk/km^2 periodically would benefit vegetation by allowing a rest period from continuous browsing pressure. This may also allow retention of some species (e.g. hazelnut) that would be lost under continuous browsing pressure (Didion et al. 2009, Bugalho et al. 2013).

A disturbance regimen that includes prescribed burns and small select cuts may also stimulate and maintain germination and recruitment. Seeds have specific germination requirements which include seed bed conditions, moisture, and sunlight (White 1979, LePage et al. 2000, Nathan and Muller-Landau 2000). Disturbance such as burning removes duff, exposing mineral soil which is required by some species to successfully germinate (e.g. *Populus tremuloides*). Small select cuts mimic tree fall and open canopy gaps for shade intolerant species and improved recruitment of shade tolerant species (Brokaw 1985, Canham et al. 1990, Wright et al. 1998). Such forest management can increase both regeneration and diversity and could be utilized in exclosures to eliminate the legacy effect or continued lack of species richness (Royo et al. 2010).

An evaluation of the seed bank may be beneficial to provide additional potential for regeneration. If such an evaluation suggests loss of species, tree plantings may be used for forest restoration, but this option may not be economically or logistically feasible. Further, plantings in combination with small cuts may also increase regeneration and restore species diversity.

Future work should include efforts to disentangle mechanisms driving plant-plant interactions (e.g., competition) in multi-ungulate systems. Our results suggest that ungulate densities of 20 animals per herd of bison, elk, and deer may allow for forest regeneration, but may not provide plant diversity necessary for multi-use preserves.

LITERATURE CITED

Abrams, M. D., and S. E. Johnson. 2012. Long-term impacts of deer exclosures on mixed-oak forest composition at the Valley Forge National Historical Park, Pennsylvania, USA 1. The Journal of the Torrey Botanical Society 139:167-180.

Allombert, S., S. Stockton, and J.-L. Martin. 2005. A natural experiment on the impact of overabundant deer on forest invertebrates. Conservation Biology 19:1917-1929.

Anderson, D. R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, USA.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management 63:247-300.

Augustine, D. J., L. E. Frelich, and P. A. Jordan. 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecological Applications 8:1260-1269.

Augustine, D. J. a. M., S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165-1183.

Bachand, M., S. Pellerin, S. D. Côté, M. Moretti, M. De Cáceres, P.-M. Brousseau, C. Cloutier, C. Hébert, É. Cardinal, and J.-L. Martin. 2014. Species indicators of ecosystem recovery after reducing large herbivore density: Comparing taxa and testing species combinations. Ecological Indicators 38:12-19.

Baiser, B., J. L. Lockwood, D. La Puma, and M. F. Aronson. 2008. A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biological Invasions 10:785-795.

Baskin, C. C., and J. M. Baskin. 2001. Seeds: ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, California, USA.

Bellingham, P., and C. Allan. 2003. Forest regeneration and the influences of white-tailed deer (*Odocoileus virginianus*) in cool temperate New Zealand rain forests. Forest Ecology and Management 175:71-86.

Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the Interior West. Conservation Biology 11:315-327.

Beschta, R. L., and W. J. Ripple. 2009. Large predators and trophic cascades in terrestrial ecosystems of the western United States. Biological Conservation 142:2401-2414.

Beschta, R. L., and W. J. Ripple. 2014. Divergent patterns of riparian cottonwood recovery after the return of wolves in Yellowstone, USA. Ecohydrology.

Bezkorowajnyj, P., A. Gordon, and R. McBride. 1993. The effect of cattle foot traffic on soil compaction in a silvo-pastoral system. Agroforestry Systems 21:1-10.

Billick, I., and T. J. Case. 1994. Higher order interactions in ecological communities: what are they and how can they be detected? Ecology 75:1529-1543.

Bjorkbom, J. C., D. A. Marquis, and F. E. Cunningham. 1965. Variability of paper birch, seed production, dispersal, and germination. Food and Agriculture Organization of the United States. U.S. Forest Servie Research Paper NE-41. Northeastern Forest Experiment Station, Upper Darby, PA.

Bonner, F. T. 2008. The woody plant seed manual. *in* R. P. Karrfalt, editor. United States Department of Agriculture. Agriculture Handbook 727.

Boulanger, V., C. Baltzinger, S. Saïd, P. Ballon, J.F. Picard, and J.L. Dupouey. 2009. Ranking temperate woody species along a gradient of browsing by deer. Forest Ecology and Management 258:1397-1406.

Brokaw, N. V. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682-687.

Brooks, R. T. 1999. Residual effects of thinning and high white-tailed deer densities on northern redback salamanders in southern New England oak forests. The Journal of Wildlife Management 63:1172-1180.

Brookshire, J. E., B. J. Kauffman, D. Lytjen, and N. Otting. 2002. Cumulative effects of wild ungulate and livestock herbivory on riparian willows. Oecologia 132:559-566.

Bugalho, M. N., I. Ibáñez, and J. S. Clark. 2013. The effects of deer herbivory and forest type on tree recruitment vary with plant growth stage. Forest Ecology and Management 308:90-100.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, USA.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Volume 1. Conifers. Agriculture Handbook, Washington, USA.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620-631.

Chao, A., R. K. Colwell, C. W. Lin, and N. J. Gotelli. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology 90:1125-1133.

Chollet, S., C. Baltzinger, L. Ostermann, F. Saint-André, and J. L. Martin. 2013. Importance for forest plant communities of refuges protecting from deer browsing. Forest Ecology and Management 289:470-477.

Collard, A., L. Lapointe, J.-P. Ouellet, M. Crête, A. Lussier, C. Daigle, and S. D. Côté. 2010a. Slow responses of understory plants of maple-dominated forests to white-tailed deer experimental exclusion. Forest Ecology and Management 260:649-662.

Collard, A., L. Lapointe, J. P. Ouellet, M. Crête, A. Lussier, C. Daigle, and S. D. Côté. 2010b. Slow responses of understory plants of maple-dominated forests to white-tailed deer experimental exclusion. Forest Ecology and Management 260:649-662.

Coppedge, B. R., and J. H. Shaw. 1997. Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. American Midland Naturalist 138:189-196.

Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. Journal of Range Management 51:258-264.

Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113-147.

De La Cretaz, A. L., and M. J. Kelty. 2002. Development of Tree Regeneration in Fern-dominated Forest Understories After Reduction of Deer Browsing. Restoration Ecology 10:416-426.

DeCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. The Journal of Wildlife Management 58:711-718.

Didion, M., A. D. Kupferschmid, and H. Bugmann. 2009. Long-term effects of ungulate browsing on forest composition and structure. Forest Ecology and Management 258:S44-S55.

Ellison, G. N., and N. Gotelli. 2013. A primer of ecological statistics. Second edition. Sinauer, Sunderland, Massachusetts, USA.

Feldhamer, G. A., B. C. Thompson, and J. A. Chapman. 2003. Wild mammals of North America: biology, management, and conservation. Johns Hopkins University Press, Baltimore, Maryland, USA.

George, L. O., and F. Bazzaz. 1999. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. Ecology 80:846-856.

Gill, R. 1992. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry 65:363-388.

Gill, R., and G. Morgan. 2009. The effects of varying deer density on natural regeneration in woodlands in lowland Britain. Forestry 83:53-63.

Goetsch, C., J. Wigg, A. A. Royo, T. Ristau, and W. P. Carson. 2011. Chronic over browsing and biodiversity collapse in a forest understory in Pennsylvania: results from a 60 year-old deer exclusion plot. The Journal of the Torrey Botanical Society 138:220-224.

Gotelli, N., and G. Ellison. 2004. A primer of ecological statistics. Sinauer, Sunderland, Massachusetts, USA.

Greenwald, K. R., L. J. Petit, and T. A. Waite. 2008. Indirect effects of a keystone herbivore elevate local animal diversity. The Journal of Wildlife Management 72:1318-1321.

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. The Journal of Wildlife Management 60:695-713.

Horsley, S. B., and D. A. Marquis. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. Canadian Journal of Forest Research 13:61-69.

Horsley, S. B., S. L. Stout, and D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13:98-118.

Hyatt, L. A., and B. B. Casper. 2000. Seed bank formation during early secondary succession in a temperate deciduous forest. Journal of Ecology 88:516-527.

Irby, L. R., J. E. Norland, M. G. Sullivan, J. A. Westfall Jr, and P. Andersen. 2000. Dynamics of green ash woodlands in Theodore Roosevelt National Park. The Prairie Naturalist 32:77-102.

J. Teichman, K., S. E. Nielsen, and J. Roland. 2013. Trophic cascades: linking ungulates to shrub-dependent birds and butterflies. Journal of Animal Ecology 82:1288-1299.

Knight, T. M., J. L. Dunn, L. A. Smith, J. Davis, and S. Kalisz. 2009. Deer facilitate invasive plant success in a Pennsylvania forest understory. Natural Areas Journal 29:110-116.

Kowalczyk, R., P. Taberlet, E. Coissac, A. Valentini, C. Miquel, T. Kamiński, and J. M. Wójcik. 2011. Influence of management practices on large herbivore diet—case of European bison in Białowieża Primeval Forest (Poland). Forest Ecology and Management 261:821-828.

Kuiters, A., and P. Slim. 2002. Regeneration of mixed deciduous forest in a Dutch forest-heathland, following a reduction of ungulate densities. Biological Conservation 105:65-74.

Laundré, J. W., L. Hernández, and W. J. Ripple. 2010. The landscape of fear: ecological implications of being afraid. Open Ecology Journal 3:1-7.

LePage, P. T., C. D. Canham, K. D. Coates, and P. Bartemucci. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Canadian Journal of Forest Research 30:415-427.

Marquis, D. A. 1975. Seed storage and germination under northern hardwood forests. Canadian Journal of Forest Research 5:478-484.

Marquis, D. A., P. L. Eckert, and B. A. Roach. 1976. Acorn weevils, rodents, and deer all contribute to oak-regeneration difficulties in Pennsylvania. Research Paper NE-356, Forest Service. U.S. Department of Agriculture, Upper Darby, PA..

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15:278-285.

NDFS. 1994. Forest Inventory Methods Section 2101. ND Forest Service.

Newman, M., F. J. G. Mitchell, and D. L. Kelly. 2014. Exclusion of large herbivores: long-term changes within the plant community. Forest Ecology and Management 321:136-144.

Nuttle, T., E. H. Yerger, S. H. Stoleson, and T. E. Ristau. 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. Ecosphere 2:1-11.

Parsons, E. W., J. L. Maron, and T. E. Martin. 2013. Elk herbivory alters small mammal assemblages in high-elevation drainages. Journal of Animal Ecology 82:459-467.

Peterson, C. J., and W. P. Carson. 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. Canadian Journal of Forest Research 26:45-52.

Price, J. N., N. K. Wong, and J. W. Morgan. 2010. Recovery of understorey vegetation after release from a long history of sheep grazing in a herb-rich woodland. Austral Ecology 35:505-514.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Ripple, W. J., and R. L. Beschta. 2007. Hardwood tree decline following large carnivore loss on the Great Plains, USA. Frontiers in Ecology and the Environment 5:241-246.

Ripple, W. J., L. E. Painter, R. L. Beschta, and C. Gates. 2010. Wolves, elk, bison, and secondary trophic cascades in Yellowstone National Park. Open Ecology Journal 3:31-37.

Roberts, C. P., C. J. Mecklin, and H. H. Whiteman. 2014. Effects of Browsing by Captive Elk (*Cervus canadensis*) on a Midwestern Woody Plant Community. The American Midland Naturalist 171:219-228.

Rooney, T. P. 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecology 202:103-111.

Rooney, T. P., and D. M. Waller. 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181:165-176.

Royo, A. A., S. L. Stout, D. S. deCalesta, and T. G. Pierson. 2010. Restoring forest herb communities through landscape-level deer herd reductions: Is recovery limited by legacy effects? Biological Conservation 143:2425-2434.

Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. The American Midland Naturalist 146:1-26.

Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1988. Tree uprooting: review of impacts on forest ecology. Vegetatio 79:165-176.

Shelton, A. L., J. A. Henning, P. Schultz, and K. Clay. 2014. Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. Forest Ecology and Management 320:39-49.

Singer, F. J., and J. E. Norland. 1994. Niche relationships within a guild of ungulate species in Yellowstone National Park, Wyoming, following release from artificial controls. Canadian Journal of Zoology 72:1383-1394.

Šipoš, J., and P. Kindlmann. 2013. Effect of the canopy complexity of trees on the rate of predation of insects. Journal of Applied Entomology 137:445-451.

Stromayer, K. A., and R. J. Warren. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25:227-234.

Takahashi, H., and K. Kaji. 2001. Fallen leaves and unpalatable plants as alternative foods for sika deer under food limitation. Ecological Research 16:257-262.

Tanentzap, A. J., K. J. Kirby, and E. Goldberg. 2012. Slow responses of ecosystems to reductions in deer (Cervidae) populations and strategies for achieving recovery. Forest Ecology and Management 264:159-166.

Taylor, R. V., and L. Arends. 2011. An assessment of the impacts of elk, deer, and cattle herbivory on aspen and deciduous shrubs on the Zumwalt Prairie. The Nature Conservancy, Enterprise, Oregon, USA.

Terborgh, J., and J. A. Estes. 2010. Trophic cascades: predators, prey, and the changing dynamics of nature. Island Press, Washington, D.C. USA.

Thompson, K. 1987. Seeds and seed banks. New Phytologist 106:23-34.

Tremblay, J. P., I. Thibault, C. Dussault, J. Huot, and S. D. Côté. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks. Canadian Journal of Zoology 83:1087-1096.

USFWS. 2008. Sullys Hill National Game Preserve: Comprehensive Conservation Plan (CCP 2008).

Veikley, L. R. 1984. Fenced Animal Management Plan. Department of the Interior, U.S. Fish and Wildlife Service, Devils Lake, North Dakota.

Ver Hoef, J. M., and P. L. Boveng. 2007. Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? Ecology 88:2766-2772.

Whalley, W. R., E. Dumitru, and A. R. Dexter. 1995. Biological effects of soil compaction. Soil and Tillage Research 35:53-68.

White, M. A. 2012. Long-term effects of deer browsing: composition, structure and productivity in a northeastern Minnesota old-growth forest. Forest Ecology and Management 269:222-228.

White, P. S. 1979. The Botanical Review 45:229-299.

Whitford, P. B. 1949. Distribution of woodland plants in relation to succession and clonal growth. Ecology 30:199-208.

Wisdom, M. J., M. Vavra, J. M. Boyd, M. A. Hemstrom, A. A. Ager, and B. K. Johnson. 2006. Understanding ungulate herbivory-episodic disturbance effects on vegetation dynamics: knowledge gaps and management needs. Wildlife Society Bulletin 34:283-292.

Wright, E. F., K. D. Coates, and P. Bartemucci. 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Canadian Journal of Forest Research 28:1352-1364.

Table 1: Four forest habitat – treatment combinations found at SHNGP, their respective sizes, and proportion of total area they represent. Eight ha of upland hardwood grazed area was converted to an exclosure in 2008.

Forest Type	Abbreviation	Hectares	% of area
Upland Hardwood Grazed (8 ha exclosure)	UHG	114 (106)	0.46 (0.43)
Upland Hardwood Ungrazed	UHUG	28	0.11
Bottomland Hardwood Grazed	BHG	52	0.21
Bottomland Hardwood Ungrazed	BHUG	55	0.22
[Prairie inside fence]		[12]	

Table 2: Animal Unit Month Conversion Table. Animal unit months (AUMs) for ungulate herds at Sullys Hill National Game Preserve (SHNGP; 3.24 km) based on Bork et al. (2013) conversions for ungulates to equivalents of one 1000 pound cow and one calf (1 AUM).

	Conversion Unit	2005 Ungulate/herd	SHNGP AUMs	AUMs/km^2	2012 Ungulate/herd	SHNGP AUMs	AUMs/km^2
White-tailed deer (*Odocoileus virginianus*)	0.15	40	6	1.9	20	3	0.9
Rocky Mountain Elk (*Cervus elaphus*)	0.6	40	24	7.4	20	12	3.7
Plains Bison (*Bison bison*)	1	40	40	12.3	20	20	6.2
Total AUMs			70	21.6 (22)		35	10.8 (11)

Table 3: Common names, abbreviations, and scientific names of shrubs and trees measured at SHNGP.

Common Name	Abbreviation	Scientific Name
Bur Oak	BO	*Quercus macrocarpus*
Basswood	BW	*Tilia americana*
Green Ash	GA	*Fraxinus pennsylvanica*
Boxelder	BX	*Acer negundo*
American Elm	AE	*Ulmus americana*
Ironwood	IW	*Ostrya virginiana*
Trembling Aspen	TA	*Populus tremuloides*
Cottonwood	TA	*Populus deltoides*
Chokecherry	CC	*Prunus virginiana*
Snowberry	SB	*Symphoricarpos albus*
Juneberry	JB	*Amelanchier sp.*
Hazelnut	HN	*Corylus spp.*
Honeysuckle	HS	*Lonicera spp.*
Hawthorn	HT	*Crataegus spp.*
High Bush Cranberry	HBC	*Viburnum trilobum*
Pincherry	PC	*Prunus pensylvanica*
Sarsaparilla		*Aralia nudicaulis*

Table 4: Summary statistics of tree species for each of four habitat-grazing combinations at SHNGP. See Table 3 for scientific names (2 points in UHG were reclassified into exclosure in 2012; 1 point was lost in UHUG due to boundary changes).

Habitat Type	Year	N	Tree (Seedlings/ha)	Tree Seedling Species Composition by %						
				BO	BW	GA	BX	AE	IW	TA
UHG	2005	28	0	0	0	0	0	0	0	0
UHG	2012	26	70 ± 223	78	0	0	22	0	0	0
UHUG	2005	11	118 ±303	11	40	43	0	6	0	0
UHUG	2012	10	263 ± 595	21	13	28	9	8	21	0
BHG	2005	15	55 ± 177	0	82	0	18	0	0	0
BHG	2012	15	99 ± 246	27	46	0	27	0	0	0
BHUG	2005	17	204 ± 320	31	17	35	1	10	0	6
BHUG	2012	17	250 ± 683	11	38	14	6	14	0	17
EXCLOSURE	2012	2	0	0	0	0	0	0	0	0

Table 5. Summary statistics for shrub species at each of four habitat-grazing combinations at SHNGP. See Table 3 for scientific names and abbreviations (2 points in UHG were reclassified into exclosure in 2012; 1 point was lost in UHUG due to boundary changes).

Habitat Type	Year	N	Shrub (Stems/ha)	Shrub Species composition by %							
				CC	SB	JB	HN	HS	HT	HBC	PC
UHG	2005	28	931 ± 815	74	26	0	0	0	0	0	0
UHG	2012	26	2413 ± 3408	46	54	0	0	0	0	0	0
UHUG	2005	11	445 ± 549	60	32	8	0	0	0	0	0
UHUG	2012	10	546 ± 1291	63	30	0	7	0	0	0	0
BHG	2005	15	645 ± 783	51	49	0	0	0	0	0	0
BHG	2012	15	1133 ± 1926	26	74	0	0	0	0	0	0
BHUG	2005	17	135 ± 228	31	20	9	31	7	2	0	0
BHUG	2012	17	452 ±1844	14	36	0	44	0	0	1	5
EXCLOSURE	2012	2	455 ± 1502	89	11	0	0	0	0	0	0

Table 6. Model selection using AICc for stem density at 65 points relative to predictors of habitat (upland or bottomland), treatment (grazed/browsed or reference), and year (2005, or 2012). K is number of parameters, and w_i is Akaike weights.

Model	K	AICc	ΔAICc	w_i	Deviance
Habitat + Treatment + Year	5	763.5	0.00	0.4786	59.98
Treatment + Year	4	764.3	0.80	0.3208	59.98
Treatment	3	765.7	2.20	0.1593	60.00
Year	3	771.7	8.20	0.0079	60.07
Intercept (Null)	2	772.1	8.60	0.0065	60.12
Habitat*Year	3	772.2	8.70	0.0062	60.08
Treatment*Year	3	772.6	9.06	0.0052	60.08
Habitat*Treatment	3	772.7	9.20	0.0048	60.08
Habitat + Year	4	772.9	9.35	0.0045	60.05
Habitat	3	773.3	9.80	0.0036	60.10
Habitat*Treatment*Year	3	773.9	10.40	0.0026	60.11

Table 7: Model-averaged estimates for binary covariates of treatment, year, habitat, and dispersion explaining stem density at Sullys Hill National Game Preserve.

Parameter	Estimate	Standard Error	Lower 95% CI	Upper 95% CI
Intercept	7.477	1.022	5.475	9.480
Treatment[1]	-2.797	0.904	-4.570	-1.025
Year[2]	1.968	0.922	0.161	3.776
Habitat[3]	1.558	0.921	-0.247	3.362
Dispersion	9.266	12.197	-14.640	33.172

[1]Treatment = grazed/browsed versus ungrazed (baseline)
[2]Year = 2012 compared to 2005 (baseline)
[3]Habitat = Bottomland versus upland (baseline)

Table 8. Summary statistics for individual-based sampling of tree species using Chao asymptotic estimators (Chao et al. 2009).

Treatment	n	S_{obs}	f_1	f_2	Chao1	σ^2_{Chao}
BHG 2005	49	6	1	1	6.5	1.75
BHUG 2005	68	12	3	1	16.5	51.8
BHG 2012	59	5	1	0	5	0
BHUG 2012	161	11	0	1	11	0
UHG 2005	90	3	0	0	3	0
UHUG 2005	76	8	2	0	9	0
UHG 2012	120	4	1	0	4	0
UHUG 2012	92	10	1	0	10	0

n = number of individuals collected in each habitat type and year
S_{obs} = number of species observed
f_1 and f_2 = singletons and doubletons, respectively
Chao1 = estimated asymptotic species richness
σ^2_{Chao} = variance of Chao1

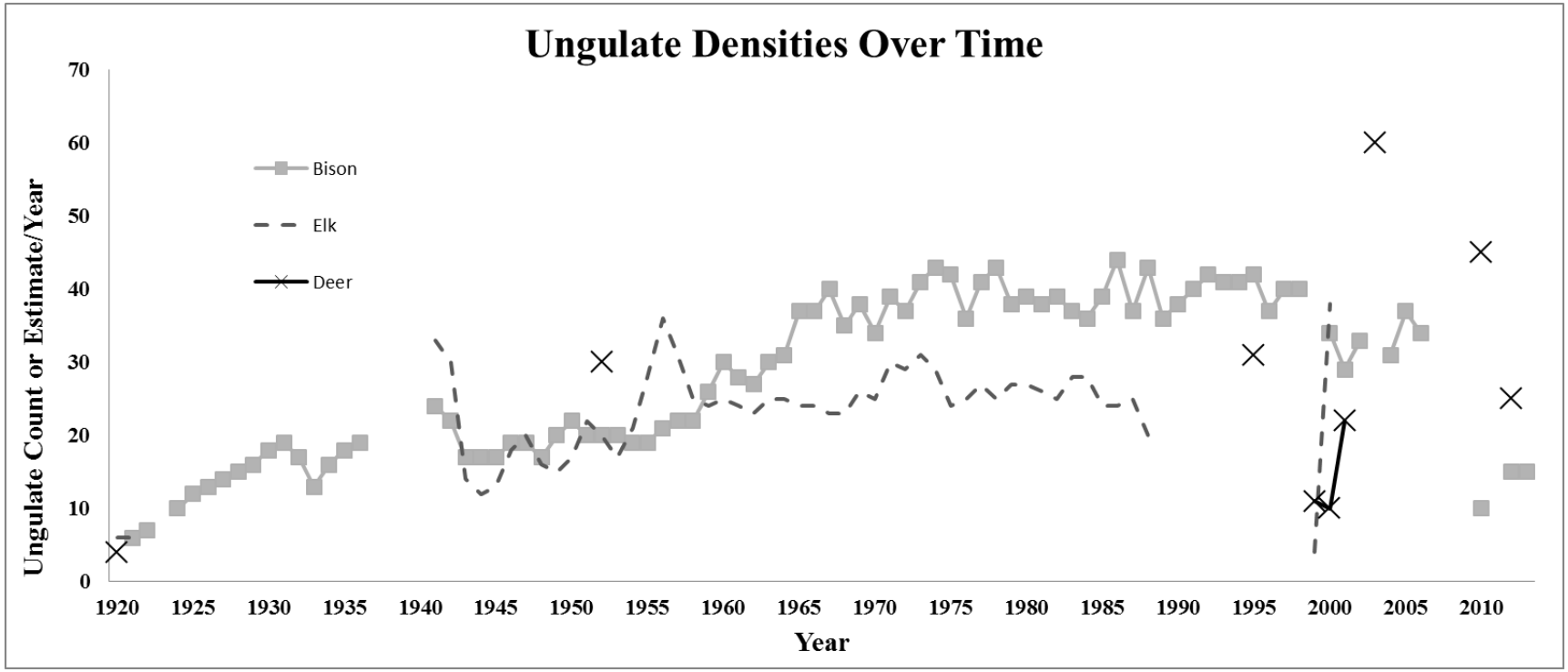


Figure 3: U.S. Fish and Wildlife survey counts of bison, elk, and deer since reintroduction in 1917. Bison counts were obtained annually, while elk and deer counts were collected less frequently. Supplementary feeding to reduce browsing pressure was started in 1958, and a 50% reduction in the herd occurred in 2008.

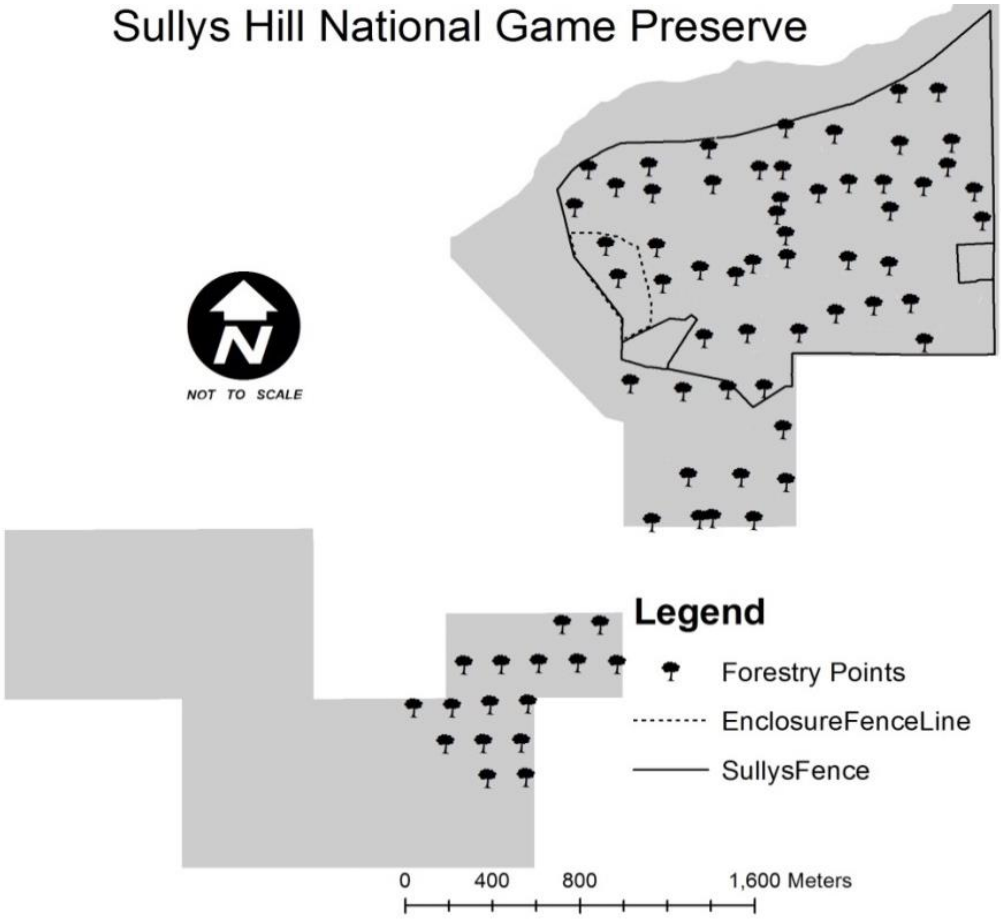


Figure 4: Seventy forest survey points collected across Sullys Hill National Game Preserve in 2005 and 2012.

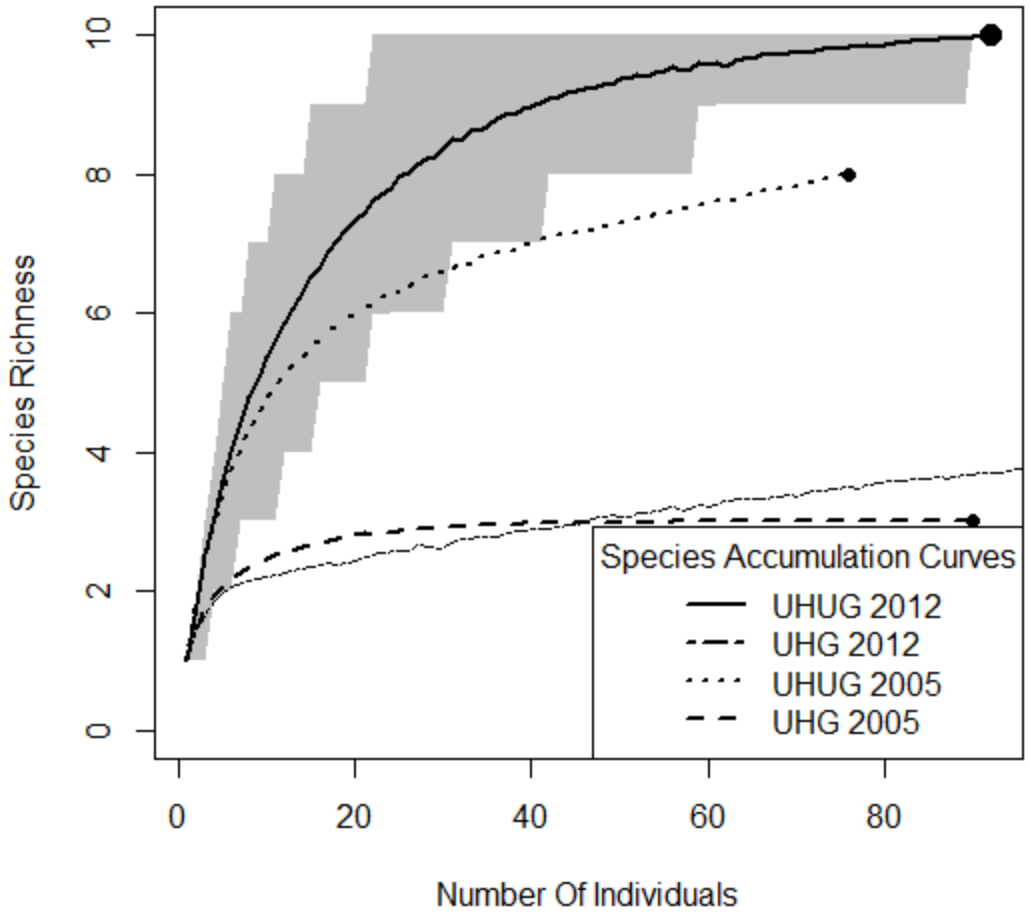


Figure 5: Individual-based rarefaction curves for grazed and ungrazed upland habitats at SHNGP. Lines represent species richness based on 1000 random subsamples from the data for each plot (n=10) in each habitat type and year.

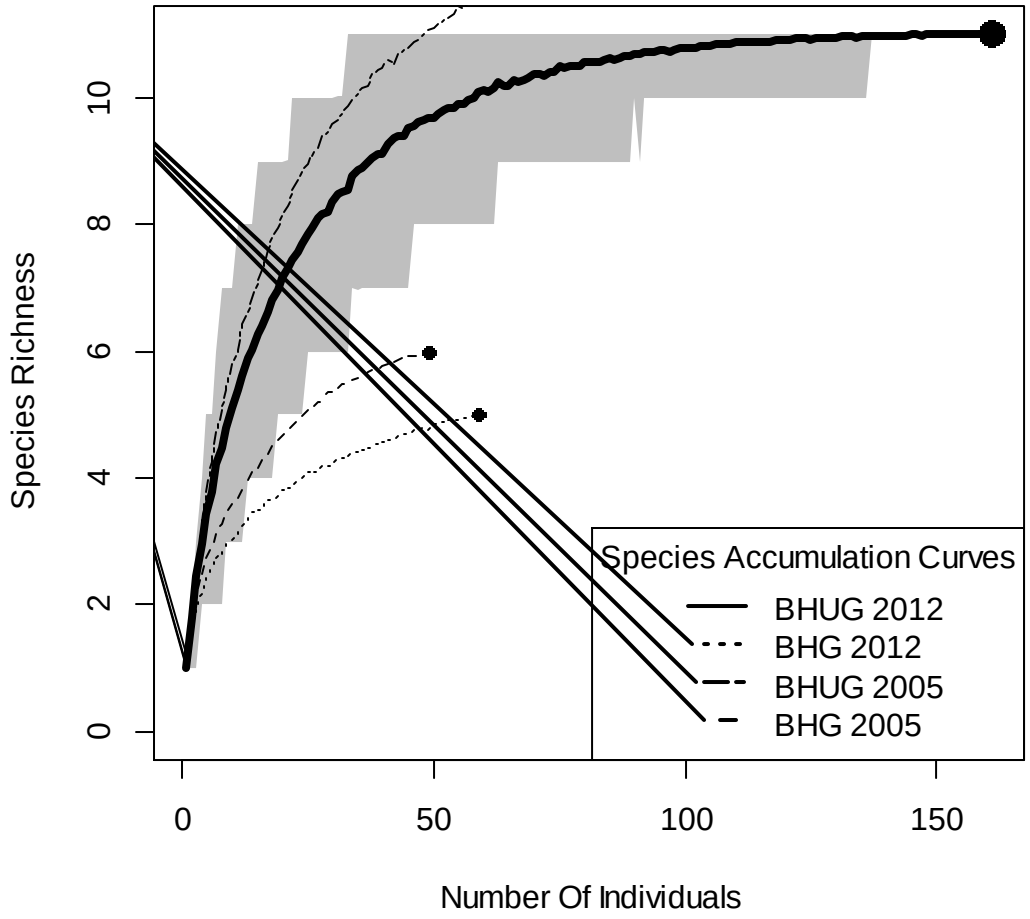


Figure 6: Individual-based rarefaction curves for grazed and ungrazed bottomland habitat at SHNGP. Lines represent species richness based on 1000 random subsamples from the data for each plot (n=10) in each habitat type and year.

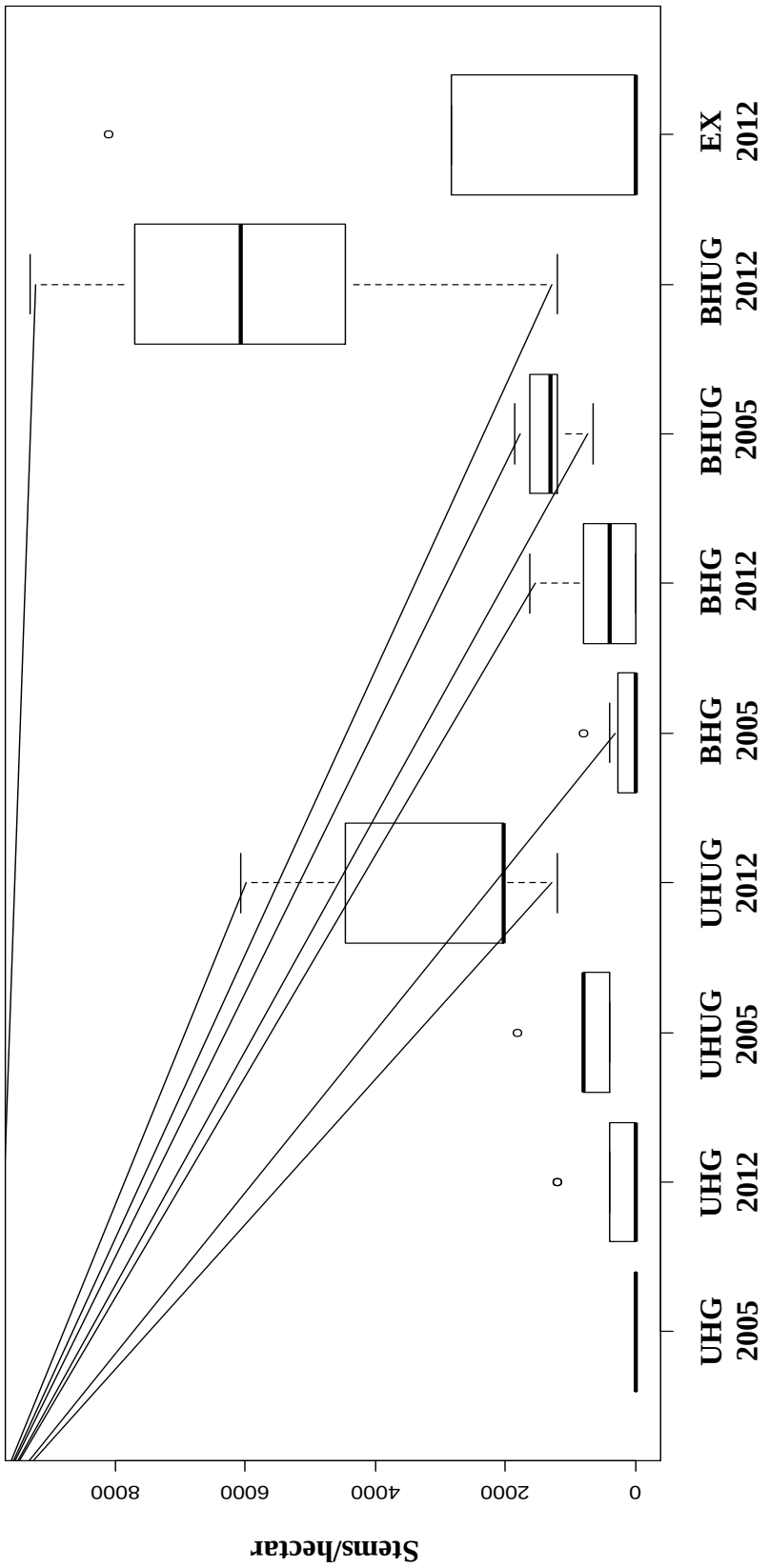


Figure 7: Boxplots of tree and shrub stem density for each habitat type and year.

CHAPTER III
PASSERINE RESPONSE TO CHANGES IN FOREST VEGETATION RESULTING FROM REDUCTION OF A MIXED UNGULATE HERD.

ABSTRACT

Bird populations are declining in forested habitats. One of the potential causes is habitat destruction due to overabundant ungulate populations. In this study we compared bird abundance of four target bird species, ovenbird (*Seiurus aurocapilla*), yellow warbler (*Dendroica petechia*), American redstart (*Setophaga ruticilla*), and red-eyed vireo (*Vireo olivaceus*), before and after a reduction of a mixed ungulate herd of Plains bison (*Bison bison*), Rocky Mountain elk (*Cervus elaphus*), and white-tailed deer (*Odocoileus virginianus*). Ungulate density was reduced in 2008 by 50% from 74 ungulates/km^2 to 37/km^2 (23 AUM/km^2 to11 AUM/km^2) in grazed areas and complete removal of ungulates from an exclosure. Three avian surveys of 57 point counts were conducted across grazing treatments (50% reduction, 100% reduction, and ungrazed reference). Royle repeat counts in program Mark were used to analyze abundance (response variable) and predictor variables grazing treatment, year (2004 2012, 2013), and habitat (upland hardwood/bottomland hardwood). We found that changes in target bird density before and after the herd reduction treatment revealed lower abundance and downward trends in ovenbird. No significant changes in abundance were observed in yellow warblers, American redstarts or red-eyed vireos, but yellow warblers and redstarts had higher abundance in exclosure (100% ungulate reduction) than grazed (50% ungulate reduction) and were similar to ungrazed abundance.

Bird abundance relative to post-herd reduction vegetation was analyzed to determine if there were specific associations with species or guilds which may be impacted by herd reduction. We found that ovenbird abundance is higher with midstory basswood saplings and native sedges and lower with native forbs. Yellow warblers had higher abundance with native sedges and lower with more midstory cover. American redstarts had higher abundance with deeper litter and lower abundance with midstory ash saplings. We found no specific vegetation associations for red-eyed vireos. Some of the associations were weakly significant and all surveys conducted at one site so there was no replication for increased inference. We concluded that more time, more browser reduction, and additional disturbance techniques may be needed to improve forest vegetation recovery and associated increases in bird abundance.

INTRODUCTION

Many forest passerine populations have declined over the past 40 years (North American Bird Conservation Initiative 2014). Given these declines, it is important to understand factors impacting their breeding habitat. Studies have demonstrated impacts of ungulates (e.g., deer and elk) on vegetation (Côté et al. 2004, Taylor and Arends 2011) that in turn can alter avian community dynamics. Composition, structure, and abundance of forest vegetation can be shaped by ungulate browsing (Horsley et al. 2003, Côté et al. 2004, Nuttle et al. 2011), but the interactions of mixed ungulate herds add a complexity that is not well understood (Latham 1999). Understanding effects of mixed ungulate herds on avian species through forest vegetation changes will improve management strategies for avian, forest, and ungulate communities.

Sullys Hill National Game Preserve (SHNGP) was established in 1904 by Theodore Roosevelt. Rocky mountain elk (*Cervus elaphus*), Plains bison (*Bison bison*), and white-tailed deer (*Odocoileus virginianus*) were reintroduced in 1918 and have been maintained at densities

resulting in moderate to high browsing pressure since 1941 (Figure 3, Chapter 2). All three ungulate herds were maintained at a density of 19 ungulates/km^2 (11 AUM/km^2: Chapter 2, Table 2) from 1941 until 1984, when a new management plan (Veikley 1984) recommended 40 animals/herd or 37 ungulates/km^2 (23 AUM/km^2). Supplementary feeding of hay and grain was added to the management regime in 1958 to reduce browsing effects in winter (Kowalczyk et al. 2011). In 2005 a forest survey conducted by the North Dakota Forest Service revealed low regeneration, and overbrowsing by ungulates was the suspected cause (Harsel 2005). In 2008 all three herds were reduced by 50%, and a 10.1 ha exclosure was added that excluded elk, bison, and deer. Reduced densities of 19 ungulates/km^2 (11 AUM/km^2) were maintained by limiting herd sizes to ≤ 20 animals/herd (USFWS 2008).

Therefore, the objective of this study was to evaluate impacts of the reduced herds on the passerine community through vegetative changes at SHNGP. Four target passerine species were selected to represent effects at different forest canopy layers and included ovenbird (*Seiurus aurocapilla*: hereafter OVEN), yellow warbler (*Dendroica petechia*: hereafter YEWA), American redstart (*Setophaga ruticilla*: herafter AMRE), and red-eyed vireo (*Vireo olivaceus*: hereafter REVI). OVEN nest and forage in the understory (Smith and Shugart 1987, Burke and Nol 1998, Seagle and Sturtevant 2005, Porneluzi et al. 2011). YEWA nest and forage in low midstory (Frydendall 1967, McPeek and Adams 1994, Lowther et al. 1999, Campbell et al. 2001). AMRE nest and forage in midstory and low canopy (Lovette and Holmes 1995, Sherry and Holmes 1997), and REVI nest and forage in high midstory and canopy (Sutton 1949, James 1976, Crawford et al. 1981, Cimprich et al. 2000).

In 2012 and 2013 we repeated bird surveys that had been conducted in 2004, pre-herd reduction, in order to answer three primary questions: 1) Has abundance changed in the target

species relative to herd reduction? 2) What is target bird abundance relative to vegetation composition and structure in the post-herd reduction conditions? 3) Has species richness changed relative to herd reduction?

METHODS

Study site. SHNGP is a located in east-central North Dakota USA, south of Devils Lake (centroid 502140, 5315194 UTM; Figure 8) with an average annual rainfall of 519 mm (CR 2014). The 676 ha refuge contains a 324 ha fenced enclosure that holds semi-free ranging elk, bison, and deer. Two forest habitat types, upland and bottomland hardwood, are present inside and outside the enclosure. These two habitats were further delineated into grazed and ungrazed areas. Although this study is looking at the effects of both browsing and grazing, we will use rangeland terminology and refer to the habitats as follows: upland hardwood grazed (UHG), upland hardwood ungrazed (UHUG), bottomland hardwood grazed BHG, and bottomland hardwood ungrazed (BHUG). Dominant species in upland hardwood include bur oak (*Quercus macrocarpus*) and green ash (*Fraxinus pennsylvanica*). Bottomland hardwood contains basswood (*Tilia americana)*, green ash, boxelder (*Acer negundo*) and American elm (*Ulmus americana*). The exclosure or 10.1 ha area fenced to exclude bison, elk, and deer, will be used in two different contexts. For evaluating changes in bird abundance, the exclosure will represent a third grazing treatment, heavily grazed then rested from grazing (100% ungulate reduction) at the same time the grazed areas received a 50% herd reduction. For models analyzing specific vegetation impacts on bird abundance, the exclosure will be treated as a fifth habitat type because grazing treatment is different than in the other four habitat types, UHG, UHUG, BHG, and BHUG.

Field Methods: Bird survey points were proportionally distributed across the four habitat types (Table 1, Chapter 2). Baseline surveys performed in 2004 used 25 points. In 2012, an additional 32 points were added to provide a more rigorous sampling effort of forest birds across the preserve. We conducted 50 m radius point counts (area = 0.8 ha), recording visual and aural observations of singing males. Surveys were repeated three times between May 24 and July 7. A survey period of sunrise to 11 am was broken into three time periods: 5 – 7am, 7 - 9am, and 9 – 11am. Each point was surveyed once in each time period in a randomized order.

In addition to bird counts, we conducted vegetation surveys of each canopy layer at each point used for bird surveys in 2012 and 2013. Canopy layers were defined as: understory < 1.5 m height, midstory 1.5 m – 7 m height, and canopy > 7 m height. We conducted a modified Daubenmire cover method (Daubenmire 1959) to evaluate the understory vegetation. This consisted of two 10 meter transects aimed along four cardinal directions and crossed at 5 m. A 20 cm x 50 cm quadrat was evaluated along each transects at 1 m and 5 m from the center point. The percent cover, dominant species, and litter depth was recorded and averaged for each point. Midstory vegetation measurements consisted of two 50 m transects positioned across the center and aimed along the four cardinal directions, dividing the area around point center into four quadrants, 25m x 25m. Dominant species and percent midstory vegetation was estimated for each quadrant, and averaged for that point. Canopy closure was estimated by placing a convex spherical densiometer on a tripod 1.4 m above the forest floor. Four readings were taken along the four cardinal directions, averaged, and multiplied by 1.04 to get percent open canopy. Closed canopy cover was calculated by subtracting percent open canopy from 100% (Lemmon 1956, Strickler 1959, Pleus and Schuett-Hames 1998). Canopy species composition was evaluated using a point-sampling method with variable plots, the method used by North Dakota Forest

Service. This method allowed us to determine a tree density using Cruz angles. Trees counted were also speciated. Biltmore sticks were used to determine diameter at breast height (Burns and Honkala 1990, NDFS 1994). Percent species was based on the number of trees identified at each point.

Data Analysis: We hypothesized an increase in abundance of OVEN, YEWA and AMRE in 2012/2013 as compared to 2004 as a result of increased regeneration in the ungrazed areas (see Chapter 2). We hypothesize no change in REVI abundance since canopy layer was unlikely to show effects due to changes in regeneration over such a short time horizon. Repeated surveys allowed detection to be incorporated into the abundance estimation using Royle repeat count methodology (Royle and Nichols 2003) with a Poisson distribution. To evaluate changes in bird abundance before and after herd reduction, we used a two stage modeling process. First, we explored covariates influencing individual bird detection (r; grazing treatment, habitat, and/or year) while holding abundance (Lambda) constant in program Mark (White and Burnham 1999). The top model (based on individual or combinations of predictors) was then used to evaluate covariates (e.g., grazed, ungrazed, exclosure, year, and habitat) relative to abundance for each target bird species. Model selection was based on Akaike's Information Criterion scores corrected for small sample size (AICc) (Akaike 1974, Burnham and Anderson 2002). Model-averaged detection parameters, beta estimates, and densities were calculated based on the top 95% of all models in the candidate set.

Using the post-reduction data only, we hypothesized that plant community composition and structure might influence target species abundance relative to grazing treatment and habitat type. We used the same two stage modeling process as we used to determine post-reduction effects, but explored vegetation covariates (Table 9) collected at bird survey points to evaluate

effects on detection and abundance. We tested for multi-collinearity and removed highly correlated vegetation covariates using a conservative cutoff value of $r^2 \geq 0.3$ (Moore and McCabe 1989). Collinear variables removed from data sets included % leafy spurge and % dogbane from understory, % chokecherry and % boxelder from midstory, and % basswood from canopy. Variables used to represent collinear pair included % smooth brome, % poison ivy, % midstory, % boxelder, and % oak, respectively. We used model-averaging to obtain detection, beta estimates and density estimates based on the top 95% of models.

We hypothesized that avian species richness would increase across SHNGP as a whole because there would be more habitat heterogeneity with a return in regeneration due to herd reduction. To estimate species richness, we constructed species accumulation curves based on four survey sampling points, the least common number to the five habitats (Ellison and Gotelli 2013). We corrected for sampling effort using individual based rarefaction (Gotelli and Colwell 2001) with program R (version 3.0.1). Species accumulation curves were estimated separately for year (2004, 2012, 2013) and habitat type (EX, UHG, UHUG, BHG, BHUG). Upland 2012 and bottomland 2012 were used as the reference curves. Asymptotic estimation of maximum number of species was calculated using Chao equations (Chao et al. 2009) and additional number of individuals that would need to be collected to capture those asymptotes. This method uses presence of singletons (species in sample represented by one individual) and doubletons (species in sample represented by two individuals) as an adequate demonstration of common and rare species. Survey data for UHUG 2004 had only one point and was not included in the accumulation curves.

We calculated summary statistics for vegetative characteristics across the habitat types. Differences in vegetation were evaluated by comparing means and standard errors of individual

species, growth habits (% sapling, % shrub, % native and non-native graminoid, % forbs), and total % cover of each canopy layer for each habitat type and grazing treatment.

RESULTS

Vegetation Characteristics By Canopy Layer

Understory: Litter depth was similar across the five habitat types (Figure 9a). We found varying amounts of native sedges across the five habitat types, but the highest amounts were in the grazed habitats (UHG, BHG, EX). Non-native graminoids were only found in grazed habitats (Figure 9b). UHG, BHG, and EX were dominated by graminoids and ungrazed habitat types (i.e, UHUG, BHUG) were dominated by forbs (Figure 9c). We found shrub composition was the least common vegetation type in all five habitats, and seedlings were found in ungrazed habitats and UHG.

Midstory: The average percent midstory and average species richness (Figure 10a and 10b) was compared across the five habitat types. There is overlap of standard error for most, but not all habitat types in both percent midstory and species richness.

Canopy: We found similar canopy species richness numbers (Figure 11a) and percent canopy closure (Figure 11b) across all five habitat types.

Before-After Herd Reduction

Bird Community: We observed a total of 212 bird species across SHNGP (Table 24). Species composition was similar across the five habitat types between 2004 and 2012/2013 (Table 10). The number of survey points used in 2012/2013 was greater, and as expected, we found more species corresponding to the increased sampling effort. Additional survey points in 2012/2013 included areas near wetlands resulting in more wetland species such as black-crowned night heron, marsh wren, and sedge wren (Table 24: scientific names). In addition to the

species observed at survey points, we found other species such as sora (*Porzana carolina*), American bittern (*Botaurus lentiginosus*), and bufflehead (*Bucephala albeola*) between survey points (Table 25: scientific names). Abundance relative to year and grazing treatment type (grazed, ungrazed, and exclosure) revealed the following changes in target bird species.

OVEN: Eleven candidate models were constructed to evaluate abundance for OVEN (Table 11). All OVEN models converged. Year was the highest ranking covariate affecting detection with no significant effect (zero encompassed in 95% confidence interval) between 2004 and 2012/2013, but a possible downward trend between 2004 and 2013 (Table 12). Year and habitat were in the both top models (top 95%) as abundance covariates (λ) with grazing treatment (g) in second ranked model (Table 11). Model-averaged estimates of year, habitat, and grazing treatment showed a significantly lower abundance between 2004 and 2012, with a possible downward trend between 2004 and 2013(Table 13). Model-averaged estimates of abundance/survey point was 0.8 – 1.0 birds/0.8 ha and a detection rate of 34% (Table 14).

YEWA: We constructed 11 models to evaluate yellow warbler abundance of which only six converged (Table 11). Habitat was the highest ranking covariate affecting detection with no significant difference in model-averaged covariates of bottomland hardwood and upland hardwood forest habitat (Table 12). Habitat and grazing treatment covariates were in the top 95% of models (Table 11). Parameter estimates showed significantly lower abundance in bottomland as compared to upland habitat (Table 13). There was no significant difference (zero encompassed in 95% confidence interval) between grazed and ungrazed treatments, but significantly higher abundance in the exclosure as compared to ungrazed treatment (Table 13). Model-averaged estimates of density were 4.5 – 5.0 birds/0.8 ha across treatment areas with a detection rate of 43% (Table 14).

AMRE: Eight of the 11 models we constructed to evaluate AMRE abundance converged (Table 11). Grazing treatment was the highest ranking covariate affecting detection (Table 11) with significantly lower detection in grazed as compared to ungrazed (Table 12). There was no significant difference between the exclosure and ungrazed treatment areas (zero encompassed in 95% confidence interval) (Table 12). Habitat was the covariate in the only model ranking above the null model (Table 11). Model-averaged estimates based on the top 95% of all models demonstrated no significant difference between upland and bottomland habitats and no significant difference between years 2004 and 2012/21013 (Table 13). Abundance was significantly lower in the grazed area as compared to ungrazed and no difference between exclosure and ungrazed (Table 13). Model-averaged estimates of density were 8.2 – 10.9 birds/0.8 ha with detection rates of 2 – 9% across treatment areas (Table 14).

REVI: Eight models converged of the 11 models constructed to evaluate REVI abundance (Table 11). Year was the highest ranking covariate affecting detection with lower trending detection in 2012 and significantly lower detection in 2013compared to 2005 (Table 12). Year and habitat as highest ranking model variables affecting abundance (λ) were in four of the top 95% of models, but were not significant when model-averaged estimates calculated (Table 13). Model-averaged estimates of density were 2.2 – 2.3 birds/0.8 ha across treatment types with a detection rate of 41% (Table 14).

Vegetation Based Models from Post-herd Reduction Sampling

OVEN: Since OVEN birds were hypothesized to be most influenced by the understory and midstory, we constructed 30 models using understory and midstory vegetation metrics (Table 26). The top 95% of candidate models included covariates of native forbs, bluegrass, smooth brome, midstory bass, canopy closure, and midstory elm as possible drivers of OVEN

abundance (Table 15; see Table 9 for scientific names). Sarsaparilla was the highest ranking variable affecting detection (Table 15) with significantly higher detection rates in higher percent sarsaparilla (Table 16). Model-averaged estimates that were significant (zero not encompassed by confidence interval) included native forb, midstory bass, and sedges (Table 19). A decrease in abundance was found relative to percent native forbs and an increase in abundance was found with increasing midstory basswood and sedge metrics. Densities based on model-averaged estimates were 0.8 birds/0.8 ha with a detection rate of 23% across habitat types (Table 20).

YEWA: Twenty five models were constructed using understory and midstory vegetation metrics (Table 25). The top 95% of models included covariates of habitat, litter depth, percent sarsaparilla cover, and percent midstory cover describing abundance (Table 17). Detection was best described by year (Table 18). Model-averaged beta estimates suggested a decrease in abundance with increasing percent midstory and an increase in abundance with increasing percent sedge (Table 19). Densities based on model-averaged estimates were 3.9 birds/0.8 ha with a 48% detection rate (Table 20).

AMRE: We constructed 17 models using understory, midstory, and canopy vegetation metrics (Table 25) to explore abundance of AMRE, and found one model carried 99% of model weight (Table 17). This model included the covariates of year, litter depth, percent understory, percent midstory, percent midstory ash, percent midstory hazel, and canopy closure, describing abundance with habitat type describing detection. UHG and BHG had lower detection compared to the baseline EX (Table 18). Increased abundance was observed with increasing litter while increasing midstory ash decreased AMRE abundance (Table 19). Density estimates of AMRE were 7 birds/0.8 ha at SHNGP with detection rates ranging from 2.7% – 12% (Table 20).

REVI: We used midstory and canopy vegetation metrics to construct 22 models for REVI abundance (Table 26). Of the top 95% of models, year and canopy covariates had the most support for describing REVI abundance (Table 17) while percent canopy best described detection. Model-averaged detection covariates of canopy and year were not significant (Table 18). All model-averaged beta estimates from the top 95% of models included zero within the 95% confidence interval suggesting no strong relationships between the predictor variables for both abundance and detection (Table 19). Densities based on model averaged estimates of real numbers were 1.8 birds/0.8 ha with a detection rate of 44 % (Table 20).

Species accumulation curves showed no difference across upland (Figure 12) and bottomland habitats (Figure 13). Asymptote or maximum species was reached for all habitat types in 2013, but additional samples appear to be needed for 2004 and 2012 habitat types (Table 21).

DISCUSSION

Has abundance changed in response to tri-herd reduction?

Differences across the three grazing treatments coupled with covariate year in top abundance models would indicate changes in individual bird abundance due to herd reduction. We observed these two variables in top models of OVEN and REVI; however, in both instances the abundance between 2004 and 2012/2013 was not significantly changed across both year and grazing treatment. OVEN and REVI abundance were lower or trending lower between years instead of the predicted increase for OVEN abundance and no change for REVI abundance. With YEWA and AMRE, there was a significant difference in the abundance across grazing treatment, but not between years, suggesting that these two species may be redistributing in response to changes in midstory vegetation, e.g. more midstory vegetation, therefore higher abundance in

exclosure. The exclosure was initially grazed upland with complete removal of ungulates allowing increases in midstory vegetation comparable to that of ungrazed areas, thus creating more nesting and foraging habitat for YEWA and AMRE.

Our results of grazing treatment effect on the four target bird species are inconsistent with similar studies that used exclosures from deer (McShea and Rappole 2000) or enclosures with multiple deer densities (DeCalesta 1994). Both of these studies found increases in midstory bird species, and McShea and Rappole (2000) also found increased abundance in understory species which included OVEN. Possible reasons for discrepancies in our results as compared to these two studies include: 1) longer temporal scale of high ungulate densities at SHNGP (60 years of 11 – 22 AUM/km^2), 2) not enough time allowed for vegetation regrowth between herd reduction and re-evaluation of avian abundance (6 – 7 years), 3) a lag time between avian abundance changes and vegetation regrowth, 4) differences in study design, and 5) limitations of our pre-herd reduction dataset including only a single year of data, and 6) natural stochasticity due to climate variation. Spring 2012 was the earliest on record as determined by ice out date and spring 2013 was one of the latest on record. For avian species whose phenology is determined by climate instead of day length, this may potentially influence breeding numbers between years (Frederiksen et al. 2004, Marra et al. 2005).

In particular, our study design compared to other research may have resulted in the different outcomes we observed. McShea and Rappole (2000) evaluated bird abundance with mist netting after nine years of complete deer exclusion (control sites: 3.7 AUM/km2). DeCaleste (1994) used a ten year treatment interval with varying deer densities (0.6 – 3.7 AUMS), and point counts were analyzed without correcting for detection. Our pre-herd reduction data only included one year of data at a limited number of sites. Further, this dataset did not

include any specific vegetation covariates, allowing us to explore finer scale vegetative changes that may allow us to monitor the responses of all of the canopy layers to the grazing treatments.

We also compared abundance trends on SHNGP to the North American Breeding Bird Survey (NABBS) trends of North Dakota. Differences in methodology and analysis between NABBS and SHNGP allow a qualitative, not quantitative comparison (Sauer et al. 2014). AMRE and REVI were similar between surveys with no significant trend (zero encompassed in 95% confidence interval). OVEN abundance is lower or trending lower at SHNGP, but no trend with NABBS (zero encompassed in 95% confidence interval). YEWA abundance appears unchanged at SHNGP, but has a positive per NABBS. Little has been reported on the status of the forest birds in North Dakota since the turn of the century with the exception of the NABBS and the NABBS categorizes the forest surveys as data with deficiency or less than 14 routes. Because of this, it is difficult to determine if the downward trend in OVEN is localized or occurring on a broader scale. More survey work is needed at a larger scale across North Dakota.

The covariate habitat was in the top models for all four birds. The analysis was comparing abundance between bottomland and upland (baseline) forest habitat. By reviewing the summary statistics of vegetation, we see that possible differences between these habitats are in the graminoid composition of the understory and species composition of all three canopy layers. This suggests that vegetation species and its subsequent structure are as important as the structure itself at each vegetation layer. By looking at bird abundance relative to specific vegetation composition, we have found some significant associations which may explain why habitat type is in the top models for these birds.

***What is target bird abundance relative to vegetation composition and structure in post-herd reduction conditions*?**

During our post-herd reduction vegetation surveys, we found differences in the understory composition across the five habitats. In particular, forbs and seedlings were highest and graminoids lowest in the ungrazed forest. Further, seedlings were absent from the exclosure and BHG areas. Millington et al. (2011) found that poor regeneration (<25% of trees) had a greater than expected impact on birds, especially early successional birds such as AMRE. For example, a reduction of regeneration from 50% to < 25% was associated with 30% reduction of early successional bird species (Millington et al. 2011). Low densities of shrubs and seedlings indicate a lack of regeneration, or that there may still too many browsing ungulates.

To evaluate midstory differences, we looked at percent cover and species richness together. Difference in species richness may be linked to browsing since several of these species would be preferred browse by deer and elk (Augustine 1998). Both YEWA and AMRE had percent midstory in top models, but OVEN and AMRE had specific effects due to individual plant species in midstory. This suggests that the presence of midstory is important to all three, but specific species such as midstory basswood and midstory ash have positive and negative effects on abundance with OVEN and AMRE respectively.

Average canopy closure and canopy species richness were similar across all habitat types. This is consistent with no change in disturbance patterns due to browsing over the last 67 years. This likely resulted in a more homogenous canopy structure due to lack of recruitment of seedlings and saplings into the canopy. None of the parameters we tested indicate either species or structure of canopy influenced REVI abundance, and this may be due to a lack of structural variation within our dataset. With a reduction in ungulates and an increase in seedlings in the

grazed areas we may see a change in canopy structure and composition in the future (Frelich and Lorimer 1985).

OVEN and YEWA showed responses relative to vegetation which may be linked to changes in grazing/browsing across the five habitats. When we evaluated OVEN abundance relative to vegetation, we found higher abundance when understory composition consisted of native sedges. We also found higher OVEN abundance trends with decreasing non-native graminoids. Bison may continue to shift the graminoid composition through selective grazing thus creating less suitable habitat for OVEN. Bison also increase percent forbs in understory composition by selectively grazing graminoids (Knapp et al. 1999), and we found OVEN abundance decreases with increasing forb content. OVEN young forage along the understory and so parental choice of nesting habitat may reflect the need for less dense grasses/forbs and cover provided by plants such as sarsaparilla and midstory basswood saplings (Burke and Nol 1998, Burke and Nol 2000, Seagle and Sturtevant 2005). Increased abundance with increased canopy closure supported results from Seagle and Sturtevant (2005) study in which they found OVEN to prefer more closed canopy, possibly related to increased insect production.

OVEN and YEWA contained habitat type in models that ranked above the null model. Since there are differences between upland and bottomland vegetation composition, it is not surprising that this would be an explanatory variable for some of our target species. Based on our model-averaged beta estimates, we found a trend towards lower abundance in bottomland hardwood areas relative to uplands for YEWA abundance and significantly higher in bottomland hardwood for OVEN. Since these two species represent understory and low midstory, they may be indicators of structural and compositional differences between upland and bottomland habitats. Vegetation may be more heavily browsed in the bottomland because of heavier

densities of deer and elk. Based on our observations and those of refuge staff, elk and deer are more commonly found in the bottomland and may have an increased impact because of higher habitat use. This may reduce nesting and foraging sites for YEWA because of impact on low midstory, but create understory sites for OVEN because of reduced competition for light and resources with midstory plants. The diverse response of these two bird species indicates the continued need for habitat heterogeneity.

We found litter depth as a predictor of AMRE abundance; however, we observed little variation in litter depth across habitat types and thus, did not appear to be linked to grazing pressure. Litter depth is usually lower in the presence of deer (Bressette et al. 2012, Lessard et al. 2012), elk (Tiedemann and Berndt 1972), and bovids (Hayes and Holl 2003), so we expected to see more variation between grazed and ungrazed habitats at SHNGP. Litter depth is associated with insect production (Bressette et al. 2012) and may influence parental preference of AMRE when searching for nesting sites (Seagle and Sturtevant 2005).

Similar to our before-after evaluations, the predictor variables we measured did not explain variation in REVI abundance with the vegetation models. In fact, the null model best explained REVI abundance which does follow our hypothesis that no immediate changes in canopy due to herd reduction would yield no changes in REVI abundance.

Has species richness changed in response to tri-herd reduction?

Based on the results from the species accumulation curves and the Choa1 estimates, there is no change observed in species richness across the five habitat types. This may be due to the limited vegetation delineation between the habitat types, the small number of points used to estimate species richness, or the short time horizon since ungulate herd reduction occurred.

MANAGEMENT IMPLICATIONS

Changes observed in the five habitat types indicates that there is some return of forest regeneration as a result of mixed ungulate herd reduction, but the changes are small. This study has also given us a better understanding of the effects of both vegetation composition and structure on abundance of the target bird species. By knowing more about preferred species composition, management can tailor disturbance strategies to improve habitat for birds and herbivores, as well as improve forest health. To promote the understory and low midstory species such as OVEN and YEWA, additional disturbance strategies can be combined to create more heterogeneity. We suggest fire to remove litter which creates substrate needed for some trees to germinate, as well as control non-natives and open lower canopy levels to allow light (White 1979, LePage et al. 2000), select cuts to create canopy gaps which increase light for shade intolerant species (Brokaw 1985, Canham et al. 1990), and native plantings to increase the diversity in understory and midstory. Patch-burn-grazing is a technique employed on prairie habitat that might be adapted to upland areas for control of non-native grasses and for creating oak savanna which is found in small areas of SHNGP (Allred et al. 2011). Of note, non-native graminoids were only found in the grazed areas and the exclosure. Burning combined with grazing may be used to slow the spread of non-natives.

In addition to 50% herd reductions, the Comprehensive Conservation Plan of SHNGP has an alternate combination of ungulates based on a previous carrying capacity study (USFWS 2008:45). The suggested densities for forest recovery are: 15 elk, 5 deer, and 19 bison. This will decrease the number of browsers potentially allowing more recovery of existing seedlings and saplings and increased regeneration that may result in more pronounced avian responses to ungulate management regimes. Future work should include regular monitoring of ungulate, avian

and forest species to determine if there is continued change with time and to re-evaluate management actions while accounting for annual variation in bird communities.

LITERATURE CITED

Akaike, H. 1974. A new look at the statistical model identification. Automatic Control, IEEE Transactions on 19:716-723.

Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire–grazing interaction. Ecology and Evolution 1:132-144.

Augustine, D. J. a. M., S.J. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. Journal of Wildlife Management 62:1165-1183.

Bressette, J. W., H. Beck, and V. B. Beauchamp. 2012. Beyond the browse line: complex cascade effects mediated by white-tailed deer. Oikos 121:1749-1760.

Brokaw, N. V. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682-687.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. The Auk 115:96-104.

Burke, D. M., and E. Nol. 2000. Landscape and fragment size effects on reproductive success of forest-breeding birds in Ontario. Ecological Applications 10:1749-1761.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer, New York, USA.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Volume 1. Conifers. Agriculture Handbook, Washington, USA.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, A. C. Stewart, and M. C. McNall. 2001. The birds of British Columbia. Volume 4.British Columbia Museum, Victoria, British Columbia.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620-631.

Chao, A., R. K. Colwell, C. W. Lin, and N. J. Gotelli. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology 90:1125-1133.

Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle. 2000. Red-eyed vireo (*Vireo olivaceus*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 18 September 2012.

Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113-147.

Crawford, H. S., R. G. Hooper, and R. W. Titterington. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. The Journal of Wildlife Management 45:680-692.

Daubenmire, R. 1959. A canopy-coverage method ol vegetational analysis. Northwest Science 33:43-64.

DeCalesta, D. S. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. The Journal of Wildlife Management 58:711-718.

Ellison, G. N., and N. Gotelli. 2013. A primer of ecological statistics. Second edition. Sinauer, Sunderland, Massachusetts, USA.

Frederiksen, M., M. P. Harris, F. Daunt, P. Rothery, and S. Wanless. 2004. Scale-dependent climate signals drive breeding phenology of three seabird species. Global Change Biology 10:1214-1221.

Frelich, L. E., and C. G. Lorimer. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biological Conservation 34:99-120.

Frydendall, M. J. 1967. Feeding ecology and territorial behavior of the yellow warbler. Dissertation. Utah State University, Logan, USA.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379-391.

Harsel, R. 2005. Forest resource management plan for Sullys Hill National Game Preserve. North Dakota Forest Service, State of North Dakota, Lisbon, ND, USA.

Hayes, G. F., and K. D. Holl. 2003. Cattle grazing impacts on annual forbs and vegetation composition of mesic grasslands in California. Conservation Biology 17:1694-1702.

Horsley, S. B., S. L. Stout, and D. S. DeCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13:98-118.

James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. The Wilson Bulletin 88:62-75.

Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie. BioScience 49:39-50.

Kowalczyk, R., P. Taberlet, E. Coissac, A. Valentini, C. Miquel, T. Kamiński, and J. M. Wójcik. 2011. Influence of management practices on large herbivore diet-case of European bison in Białowieża Primeval Forest (Poland). Forest Ecology and Management 261:821-828.

Latham, J. 1999. Interspecific interactions of ungulates in European forests: an overview. Forest Ecology and Management 120:13-21.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest overstory density. Forest Science 2:314-320.

LePage, P. T., C. D. Canham, K. D. Coates, and P. Bartemucci. 2000. Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. Canadian Journal of Forest Research 30:415-427.

Lessard, J.-P., W. N. Reynolds, W. A. Bunn, M. A. Genung, M. A. Cregger, E. Felker-Quinn, M. N. Barrios-Garcia, M. L. Stevenson, R. M. Lawton, and C. B. Brown. 2012. Equivalence in the strength of deer herbivory on above and below ground communities. Basic and Applied Ecology 13:59-66.

Lovette, I. J., and R. T. Holmes. 1995. Foraging behavior of American Redstarts in breeding and wintering habitats: implications for relative food availability. Condor 97:782-791.

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. 1999. Yellow warbler (*Setophaga petechia*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 19 September 2012.

Marra, P., C. Francis, R. Mulvihill, and F. Moore. 2005. The influence of climate on the timing and rate of spring bird migration. Oecologia 142:307-315.

McPeek, G. A., and R. J. Adams. 1994. The birds of Michigan. Indiana University Press. Indianapolis, Indiana, USA.

McShea, W. J., and J. H. Rappole. 2000. Managing the abundance and diversity of breeding bird populations through manipulation of deer populations. Conservation Biology 14:1161-1170.

Millington, J. D., M. B. Walters, M. S. Matonis, E. J. Laurent, K. R. Hall, and J. Liu. 2011. Combined long-term effects of variable tree regeneration and timber management on forest songbirds and timber production. Forest Ecology and Management 262:718-729.

Moore, D. S., and G. P. McCabe. 1989. Introduction to the practice of statistics. W H Freeman/Times Books/ Henry Holt & Co, New York, NY, US.

NDFS. 1994. Forest Inventory Methods Section 2101. ND Forest Service.

North American Bird Conservation Initiative, U. S. C. 2014. The State of the Birds 2014 Report. *in* U.S. Department of Interior, Washington, D.C.

Nuttle, T., E. H. Yerger, S. H. Stoleson, and T. E. Ristau. 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. Ecosphere 2:1-11.

Pleus, A., and D. Schuett-Hames. 1998. TFW Monitoring Program method manual for the reference point survey. TFW Monitoring Program, Northwest Indian Fisheries Commission.

Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2011. Oven Bird (*Seiurus aurocapilla*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 9 September 2012.

Royle, J. A., and J. D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777-790.

Sauer, J. R., J. E. Hines, J. E. Fallon, K. L. Pardieck, D. J. Ziolkowski, Jr., and W. A. Link. 2014. The North American Breeding Bird Survey, Results and Analysis 1966 - 2012. Version 02.19.2014 USGS Patuxent Wildlife Research Center, Laurel, MD. Accessed 28 November 2014.

Seagle, S. W., and B. R. Sturtevant. 2005. Forest productivity predicts invertebrate biomass and ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian landscapes. Ecology 86:1531-1539.

Sherry, T. W., and R. T. Holmes. 1997. American redstart (*Setophaga ruticilla*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 20 September 2012.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology 68:695-704.

Strickler, G. S. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. US Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station.

Sutton, G. M. 1949. Studies of the nesting birds of the Edwin S. George Reserve, Part I: The Vireos. University of Michigan Press, Ann Arbor, Michigan, USA.

Taylor, R. V., and L. Arends. 2011. An assessment of the impacts of elk, deer, and cattle herbivory on aspen and deciduous shrubs on the Zumwalt Prairie. The Nature Conservancy, Enterprise, Oregon, USA.

Team, R. C. 2013. R Foundation for Statistical Computing, Vienna, Austria.

Tiedemann, A., and H. Berndt. 1972. Vegetation and soils of a 30-year deer and elk exclosure in central Washington. Northwest Science 46:59-96.

USFWS. 2008. Sullys Hill National Game Preserve: Comprehensive Conservation Plan (CCP 2008).

Veikley, L. R. 1984. Fenced Animal Management Plan. US Department of the Interior, Devils Lake, ND.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120-S139.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. The Botanical Review 45:229-299.

Table 9: Description of vegetation covariate metrics.

Forest Layer	Covariate (abbreviation)	Scientific Name	Data Type	Description
	Year 13		categorical	Binary variable for study of years 2012 (baseline) and 2013
	Bottomland (bottom)		categorical	Binary variable for study of habitat types; upland (baseline) versus bottomland
Understory (<1.5 m)	Litter		continuous	Depth of litter (cm)
	Sarsaparillla (sarsap)	*Aralia nudicaulis*	continuous	% of understory with sarsaparilla dominated cover
	Reed Canary Grass (reed)	*Phalaris arundinacea*	continuous	% of understory with reed canary grass dominated cover
	Sedge	*Cyperaceae spp.*	continuous	% of understory with sedge dominated cover
	Native forbes (natforb)		continuous	% of understory with native forb cover, no dominant species
	Bluegrass (blue)	*Poa pratensis*	continuous	% of understory with bluegrass dominated cover
	Smooth brome (brome)	*Bromus inermis*	continuous	% of understory with smooth brome dominated cover
	Canada wild rye (rye)	*Elymus canadensis*	continuous	% of understory with Canada wild rye dominated cover
	Plantain	*Plantago major*	continuous	% of understory with plantain dominated cover
	Gooseberry spp. (goose)	*Ribes spp.*	continuous	% of understory with gooseberry spp. dominated cover
	Hazelnut spp. (hazel)	*Corylus spp.*	continuous	% of understory with hazelnut spp. dominated cover
	Snowberry (snow)	*Symphoricarpos occidentalis*	continuous	% of understory with snowberry dominated cover
	Choke cherry (choke)	*Prunus virginiana*	continuous	% of understory with choke cherry dominated cover
	Columbine (columb)	*Aquilegia canadensis*	continuous	% of understory with columbine dominated cover
	Poison ivy (pivy)	*Toxicodendron radicans*	continuous	% of understory with poison ivy dominated cover
	Raspberry	*Rubus idaeus*	continuous	% of understory with raspberry dominated cover
	Hog peanut (hog)	*Amphicarpaea bracteata*	continuous	% of understory with hog peanut dominated cover
	Woodbine (wbine)	*Parthenocissus vitacea*	continuous	% of understory with woodbine dominated cover
	Bedstraw (bed)	*Galium spp.*	continuous	% of understory with bedstraw dominated cover
	Wood sorrel (sorrel)	*Oxalis spp.*	continuous	% of understory with wood sorrel dominated cover
	Tall meadow rue (rue)	*Thalictrum dasycarpum*	continuous	% of understory with early meadow rue dominated cover

Table 9 continued.

Forest Layer	Covariate (abbreviation)	Scientific Name	Data Type	Description
	% Shrubs		continuous	Average of all woody plants across point
	% Forbs		continuous	Average of all forbs across point
	% Graminoid		continuous	Average of all graminoids across point
	% Nonnative graminoids		continuous	Average of all graminoids except sedges across point
Midstory (1.5 - 7 m)	Basswood	*Tilia americana*	continuous	% of midstory comprised of basswood
	Green ash	*Fraxinus pennsylvanica*	continuous	% of midstory comprised of green ash
	American elm	*Ulmus americana*	continuous	% of midstory comprised of American elm
	Hazelnut spp.	*Corylus spp.*	continuous	% of midstory comprised of hazelnut spp.
	High bush cranberry	*Viburnum trilobum*	continuous	% of midstory comprised of h.b. cranberry
	Aspen	*Populus spp.*	continuous	% of midstory comprised of populus spp
	Oak	*Quercus macrocarpus*	continuous	% of midstory comprised of oak
	Midstory spp. #		continuous	number of woody midstory species at each point
Canopy (>7 m)	Canopy closure		continuous	% canopy closure at each point
	Bur oak	*Quercus macrocarpus*	continuous	% of trees comprised of bur oak
	Green ash	*Fraxinus pennsylvanica*	continuous	% of trees comprised of green ash
	Aspen	*Populus spp.*	continuous	% of trees comprised of aspen
	American elm	*Ulmus americana*	continuous	% of trees comprised of American elm
	Snag		continuous	% of trees comprised of snags

Table 10: Number of birds observed based on maximum counts for each species at each point. Species number is number of species observed over all points within a habitat type.

Year		UHG	UHUG	BHG	BHUG	EX
2004	# of Survey Points	12	1	5	5	2
	Bird Occurrences	237	21	99	93	47
	Species Number	**33**	**15**	**26**	**24**	**16**
2012	# of Survey Points	23	6	11	13	4
	Bird Occurrences	569	145	282	326	96
	Species Number	**40**	**34**	**41**	**35**	**23**
2013	# of Survey Points	23	6	11	13	4
	Bird Occurrences	466	101	219	266	67
	Species Number	**42**	**25**	**40**	**40**	**22**

Table 11: Abundance models constructed using data from 2004, 2012, 2013. Data from 25 points in 2004 and 57 points in 2012 and 2013 were used for this analysis. Groups were based on grazing treatment (grazed, exclosure, ungrazed - baseline). Covariates were year (2004 – baseline) and habitat (upland - baseline, bottomland) and constant or null model (.). Symbols and abbreviations are as follows: r = detection parameter, λ = abundance parameter, K = number of parameters in a model, AICc and ΔAICc represent Akaike Information Criterion scores corrected for small sample size, W = weight of model, and L = likelihood of model.

	Model	K	AICc	ΔAICc	w	L	Deviance
OVEN	r (year) λ (habitat+year)	7	604.68	0.00	0.68	1.00	589.87
	r (year) λ (g+habitat+year)	9	606.18	1.50	0.32	0.47	586.86
	r (year) λ (habitat)	5	616.40	11.72	0.00	0.00	605.97
	r (year) λ (g)	6	616.93	12.26	0.00	0.00	604.33
	r (year) λ (g+habitat)	7	617.21	12.53	0.00	0.00	602.41
	r (year) λ (.)	4	619.14	14.46	0.00	0.00	610.86
	r (.) λ (g)	4	653.59	48.91	0.00	0.00	645.31
	r (.) λ (.)	2	654.04	49.36	0.00	0.00	649.96
	r (g) λ (.)	4	654.92	50.24	0.00	0.00	646.64
	r (habitat) λ (.)	3	655.58	50.90	0.00	0.00	649.41
	r (g) λ (g)	6	656.25	51.58	0.00	0.00	643.65
YEWA	r (habitat) λ (habitat)	4	1373.88	0.00	0.72	1.00	1365.60
	r (habitat) λ (g)	5	1376.80	2.91	0.17	0.23	1366.37
	r (habitat) λ (.)	3	1378.34	4.46	0.08	0.11	1372.18
	r (.) λ (.)	2	1381.19	7.31	0.02	0.03	1377.10
	r (g) λ (.)	4	1381.88	8.00	0.01	0.02	1373.60
	r (year) λ (.)	4	1382.93	9.05	0.01	0.01	1374.65
AMRE	r (g) λ (habitat)	5	696.60	0.00	0.46	1.00	686.18
	r (g) λ (.)	4	697.61	1.01	0.28	0.60	689.33
	r (g) λ (habitat+year)	7	699.54	2.94	0.11	0.23	684.73
	r (.) λ (g)	4	699.88	3.28	0.09	0.19	691.60
	r (g) λ (year)	6	700.62	4.02	0.06	0.13	688.02
	r (habitat) λ (.)	3	745.71	49.11	0.00	0.00	739.54
	r (.) λ (.)	2	759.59	62.99	0.00	0.00	755.51
	r (year) λ (.)	4	761.10	64.49	0.00	0.00	752.82
REVI	r (year) λ (.)	4	967.40	0.00	0.42	1.00	959.12
	r (year) λ (year)	6	968.20	0.81	0.28	0.67	955.60
	r (year) λ (habitat)	5	969.52	2.13	0.14	0.35	959.10
	r (year) λ (habitat+year)	7	970.40	3.00	0.09	0.22	955.59
	r (year) λ (g)	6	971.15	3.76	0.06	0.15	958.55
	r (.) λ (.)	2	986.08	18.68	0.00	0.00	982.00
	r (g) λ (.)	4	987.50	20.11	0.00	0.00	979.22
	r (g) λ (g)	6	990.68	23.29	0.00	0.00	978.08

Table 12: Model-averaged detection, r, estimates for before-after herd reduction models using covariates of treatment (grazed, ungrazed, exclosure), year (2004, 2012, 2013) and habitat (upland, bottomland) for four target bird species.

	Parameter	r Estimate	r SE	r LCI	r UCI
OVEN	Intercept	-0.35	0.51	-1.35	0.65
	2012	0.19	0.61	-1.00	1.38
	2013	-0.94	0.78	-2.48	0.59
YEWA	Intercept	-0.400	0.286	-0.961	0.162
	Habitat	0.338	0.467	-0.577	1.253
AMRE	Intercept	-2.386	1.157	-4.654	-0.117
	Grazed	**-1.434**	**0.214**	**-1.854**	**-1.015**
	Exclosure	-0.397	0.382	-1.146	0.351
REVI	Intercept	0.49	0.32	-0.15	1.12
	2012	-0.83	0.47	-1.75	0.08
	2013	**-1.20**	**0.54**	**-2.25**	**-0.14**

Table 13: Model-averaged parameter estimates describing the relationship between abundance and covariates of year (2004, 2012, 2013), habitat type (upland, bottomland), and treatment (grazed, ungrazed, exclosure). Model-averaged estimates are based on top 95% ranked abundance models for each target bird species. Bird species models set includes detection correction.

	Covariate	Estimate	SE	LCI	UCI
OVEN	Intercept	0.94	0.36	0.24	1.65
	Habitat	0.36	0.21	-0.05	0.77
	2012	**-1.54**	**0.38**	**-2.28**	**-0.79**
	2013	-1.02	0.56	-2.11	0.07
	Grazed	-0.33	0.22	-0.75	0.09
	Exclosure	-0.81	0.74	-2.26	0.65
YEWA	Intercept	1.67	0.20	1.29	2.06
	Habitat	**-0.57**	**0.22**	**-1.00**	**-0.14**
	Grazed	0.08	0.10	-0.12	0.28
	Exclosure	**0.47**	**0.19**	**0.10**	**0.83**
AMRE	Intercept	2.13	1.04	0.09	4.17
	Habitat	0.31	0.17	-0.03	0.64
	Grazed	**-1.40**	**0.17**	**-1.74**	**-1.06**
	Exclosure	-0.46	0.31	-1.06	0.14
	2012	0.23	0.25	-0.27	0.72
	2013	0.06	0.26	-0.45	0.57
REVI	Intercept	0.96	0.19	0.60	1.33
	Habitat	-0.02	0.14	-0.28	0.25
	Grazed	0.07	0.14	-0.21	0.34
	Exclosure	-0.15	0.34	-0.82	0.52
	2012	-0.41	0.27	-0.93	0.12
	2013	-0.58	0.30	-1.17	0.01

Table 14: Model-averaged estimates of abundance and detection based on top 95% of all models for each target bird species based on grazing treatment (grazed, ungrazed, exclosure), year (2004, 2012, 2013), and habitat type (upland, bottomland). Abundance dataset for 2004, 2012, and 2013 used for analysis and area of each survey point is 0.8 ha (50 m radius point count area).

	Parameter	Covariate	Estimate	SE	LCI	UCI
OVEN	Detection	Grazed	0.34	0.07	0.23	0.48
	Detection	Exclosure	0.34	0.07	0.23	0.48
	Detection	Ungrazed	0.34	0.07	0.23	0.48
	Lambda	Grazed	0.92	0.21	0.04	1.00
	Lambda	Exclosure	0.81	0.34	0.05	1.00
	Lambda	Ungrazed	1.03	0.28	0.48	1.58
YEWA	Detection	Grazed	0.43	0.05	0.34	0.53
	Detection	Exclosure	0.43	0.05	0.34	0.53
	Detection	Ungrazed	0.43	0.05	0.34	0.53
	Lambda	Grazed	4.56	0.54	3.50	5.63
	Lambda	Exclosure	4.95	1.14	2.71	7.18
	Lambda	Ungrazed	4.50	0.56	3.41	5.59
AMRE	Detection	Grazed	0.02	0.02	0.00	0.15
	Detection	Exclosure	0.06	0.06	0.01	0.34
	Detection	Ungrazed	0.09	0.09	0.01	0.44
	Lambda	Grazed	8.23	9.13	0.00	26.12
	Lambda	Exclosure	9.58	15.43	0.00	39.83
	Lambda	Ungrazed	10.87	22.79	0.00	55.53
REVI	Detection	Grazed	0.41	0.07	0.28	0.56
	Detection	Exclosure	0.41	0.07	0.28	0.56
	Detection	Ungrazed	0.41	0.07	0.28	0.56
	Lambda	Grazed	2.27	0.43	1.43	3.12
	Lambda	Exclosure	2.24	0.46	1.34	3.14
	Lambda	Ungrazed	2.26	0.43	1.42	3.10

Table 15: Top 95% of candidate models constructed using bird abundance data from 2012 and 2013. Vegetation metrics collected at the 57 avian survey points were used as covariates to look for relationships between avian target species and vegetation species. See Table 3 for vegetation covariate descriptions. Detection covariates were analyzed using Royle repeat counts are denoted by r ( ). Abundance and vegetation covariates are denoted with lambda, λ ( ). The 5 habitat types (exclosure, UHG, UHUG, BHG, BHUG, respectively) are represented by group (g).

	Model	K	AICc	ΔAICc	w	L	Deviance
OVEN	r (sarsap) λ (native forb+blue+brome+mbass)	7	378.85	0.00	0.39	1.00	363.79
	r (sarsap) λ (native forb+blue+brome+mbass+canopy)	8	380.64	1.79	0.16	0.41	363.27
	r (sarsap) λ (native forb+bluel+brome+mbass+melm)	8	381.04	2.19	0.13	0.33	363.67
	r (sarsap) λ (mbass)	4	382.20	3.35	0.07	0.19	373.84
	r (sarsap) λ (blue+brome)	5	382.91	4.06	0.05	0.13	372.35
	r (sarsap) λ (brome)	4	383.19	4.34	0.04	0.11	374.83
	r (sarsap) λ (melm)	4	384.40	5.55	0.02	0.06	376.03
	r (sarsap) λ (native forb)	4	384.73	5.88	0.02	0.05	376.36
	r (sarsap) λ (canopy)	4	385.46	6.61	0.01	0.04	377.10
	r (sarsap) λ (blue)	4	385.54	6.69	0.01	0.04	377.18
	r (sarsap) λ (.)	3	385.58	6.73	0.01	0.03	379.36
	r (sarsap) λ (sarsap)	4	386.07	7.22	0.01	0.03	377.70
	r (sarsap) λ (sedge)	4	386.33	7.48	0.01	0.02	377.96
	r (sarsap) λ (understory)	4	386.36	7.51	0.01	0.02	377.99
	r (sarsap) λ (litter)	4	386.71	7.86	0.01	0.02	378.34
YEWA	r (year) λ (habitat + litter + sarsap + midstory)	7	1034.05	0.00	0.25	1.00	1018.99
	r (year) λ (sarsap + forb + midstory)	6	1034.85	0.80	0.17	0.67	1022.06
	r (year) λ (litter + sarsap + midstory + mbass)	7	1035.03	0.98	0.15	0.61	1019.97
	r (year) λ (litter + sarsap + forb + midstory)	7	1035.11	1.06	0.15	0.59	1020.05
	r (year) λ (forbs)	4	1035.31	1.26	0.13	0.53	1026.94
	r (year) λ (midstory)	4	1038.22	4.17	0.03	0.12	1029.85
	r (year) λ (sarsap)	4	1038.36	4.31	0.03	0.12	1029.99
	r (year) λ (litter+sedge+brome)	6	1039.61	5.56	0.02	0.06	1026.82
	r (year) λ (litter+sedge)	5	1040.26	6.21	0.01	0.04	1029.70
	r (year) λ (litter)	4	1040.47	6.42	0.01	0.04	1032.11
AMRE	r (g) λ (year + litter + understory + midstory + mash + mhazel + canopy)	13	512.53	0.00	0.99	1.00	514.53

Table 15 continued.

	Model	K	AICc	ΔAICc	w	L	Deviance
REVI	r (canopy) λ (year)	4	708.84	0.00	0.20	1.00	700.48
	r (canopy) λ (year+canopy)	5	709.98	1.14	0.11	0.57	699.43
	r (canopy) λ (.)	3	710.09	1.24	0.11	0.54	703.87
	r (canopy) λ (year+ habitat)	5	711.00	2.16	0.07	0.34	700.45
	r (canopy) λ (year+litter)	5	711.02	2.17	0.07	0.34	700.46
	r (year) λ (.)	3	711.06	2.22	0.07	0.33	704.84
	r (canopy) λ (canopy spp #)	4	711.53	2.68	0.05	0.26	703.16
	r (canopy) λ (understory)	4	711.60	2.76	0.05	0.25	703.23
	r (.) λ (.)	2	711.90	3.06	0.04	0.22	707.79
	r (canopy) λ (midstory)	4	712.08	3.24	0.04	0.20	703.71
	r (canopy) λ (habitat)	4	712.21	3.37	0.04	0.19	703.84
	r (canopy) λ (litter)	4	712.22	3.38	0.04	0.18	703.86
	r (canopy) λ(year+exclosure+grazed)	6	712.62	3.78	0.03	0.15	699.84
	r (.) λ (canopy)	3	712.92	4.08	0.03	0.13	706.70

Table 16: Model-averaged estimates of detection, r, based on top 95% of models constructed using vegetation covariates and bird abundance. See Table 23-26 for full model sets.

	Parameter	r Estimate	r SE	r LCI	r UCI
OVEN	Intercept	-1.597	0.453	-2.486	-0.709
	Sarsap	**0.021**	**0.009**	**0.004**	**0.038**
YEWA	Intercept	-0.287	0.054	-0.392	-0.182
	Year	0.373	0.200	-0.019	0.765
AMRE	Intercept	-2.026	1.334	-4.640	0.587
	EX	-0.783	0.451	-1.668	0.102
	UHG	**-1.547**	**0.369**	**-2.269**	**-0.824**
	UHUG	-0.512	0.408	-1.312	0.287
	BHG	**-1.496**	**0.423**	**-2.325**	**-0.667**
REVI	Intercept	-1.572	1.752	-5.006	1.863
	Canopy	0.022	0.013	-0.004	0.048
	Year	-0.471	0.268	-0.997	0.055

Table 17: Model-averaged beta (β) estimates for covariates explaining abundance. Covariates are based on top 95% ranked models for each model set. Bolded terms have confidence intervals that do not include zero in the confidence interval.

	Parameter	β Estimate	β SE	β LCI	β UCI
OVEN	Intercept	-0.07	0.56	-1.16	1.02
	Native Forb	**-0.020**	**0.010**	**-0.040**	**0.000**
	Bluegrass	-0.020	0.020	-0.050	0.010
	Smooth Brome	-0.090	0.130	-0.350	0.170
	Midstory Bass	**0.030**	**0.010**	**0.000**	**0.050**
	Canopy	0.010	0.010	-0.020	0.040
	Midstory Elm	0.020	0.040	-0.050	0.090
	Sarsaparilla	0.010	0.010	-0.010	0.040
	Sedges	**0.010**	**0.010**	**0.000**	**0.020**
	Understory	-0.010	0.010	-0.030	0.010
YEWA	Intercept	1.804	0.320	1.176	2.432
	habitat	-0.128	0.118	-0.358	0.103
	Litter	0.067	0.044	-0.019	0.154
	Sarsap	-0.005	0.003	-0.011	0.001
	Midstory	**-0.007**	**0.003**	**-0.014**	**-0.001**
	Forb	-0.004	0.004	-0.012	0.004
	Mbass	-0.001	0.003	-0.007	0.004
	Sedge	**0.003**	**0.002**	**0.000**	**0.007**
	Brome	0.007	0.004	-0.001	0.015
AMRE	Intercept	1.326	1.524	-1.661	4.312
	Year	-0.184	0.178	-0.534	0.165
	Litter	**0.248**	**0.090**	**0.072**	**0.423**
	Understory	-0.005	0.007	-0.020	0.009
	Midstory	0.012	0.007	-0.003	0.026
	Midstory Ash	**-0.082**	**0.040**	**-0.160**	**-0.003**
	Hazelnut	-0.001	0.007	-0.014	0.012
	Canopy	0.005	0.007	-0.010	0.019
REVI	Intercept	0.873	0.692	-0.483	2.230
	Year	-0.305	0.165	-0.628	0.018
	Canopy Spp. #	0.133	0.159	-0.177	0.444
	Understory	0.004	0.005	-0.006	0.014
	Midstory	0.001	0.003	-0.005	0.008
	habitat	0.027	0.165	-0.297	0.351
	Litter	0.011	0.069	-0.124	0.145
	Canopy	-0.015	0.024	-0.063	0.033
	Exclosure	-0.283	0.371	-1.011	0.446
	Grazed	-0.060	0.174	-0.402	0.281

Table 18: Model-averaged estimates for abundance and detection based on top 95% of all models for each target bird species and based on vegetation and habitat covariates. See Table 3 for covariates used in top 95% models.

	Parameter	Covariate	Estimate	SE	LCI	UCI
OVEN	Detection	EX	0.231	0.066	0.127	0.384
	Detection	UHG	0.231	0.066	0.127	0.384
	Detection	UHUG	0.231	0.066	0.127	0.384
	Detection	BHG	0.231	0.066	0.127	0.384
	Detection	BHUG	0.231	0.066	0.127	0.384
	Lambda	EX	0.766	0.372	0.053	0.995
	Lambda	UHG	0.766	0.372	0.053	0.995
	Lambda	UHUG	0.766	0.372	0.053	0.995
	Lambda	BHG	0.766	0.372	0.053	0.995
	Lambda	BHUG	0.766	0.372	0.053	0.995
YEWA	Detection	EX	0.475	0.050	0.380	0.572
	Detection	UHG	0.475	0.050	0.380	0.572
	Detection	UHUG	0.475	0.050	0.380	0.572
	Detection	BHG	0.475	0.050	0.380	0.572
	Detection	BHUG	0.475	0.050	0.380	0.572
	Lambda	EX	3.900	0.429	3.060	4.741
	Lambda	UHG	3.900	0.429	3.060	4.741
	Lambda	UHUG	3.900	0.429	3.060	4.741
	Lambda	BHG	3.900	0.429	3.060	4.741
	Lambda	BHUG	3.900	0.429	3.060	4.741
AMRE	Detection	EX	0.057	0.066	0.005	0.400
	Detection	UHG	0.027	0.031	0.003	0.220
	Detection	UHUG	0.073	0.084	0.007	0.469
	Detection	BHG	0.029	0.033	0.003	0.235
	Detection	BHUG	0.116	0.137	0.010	0.643
	Lambda	EX	7.081	8.095	-8.785	22.947
	Lambda	UHG	7.081	8.095	-8.785	22.947
	Lambda	UHUG	7.081	8.095	-8.785	22.947
	Lambda	BHG	7.081	8.095	-8.785	22.947
	Lambda	BHUG	7.081	8.095	-8.785	22.947
REVI	Detection	EX	0.439	0.067	0.315	0.571
	Detection	UHG	0.439	0.067	0.315	0.571
	Detection	UHUG	0.439	0.067	0.315	0.571
	Detection	BHG	0.439	0.067	0.315	0.571
	Detection	BHUG	0.439	0.067	0.315	0.571
	Lambda	EX	1.817	0.317	1.196	2.437
	Lambda	UHG	1.828	0.299	1.242	2.414
	Lambda	UHUG	1.832	0.301	1.242	2.422
	Lambda	BHG	1.828	0.299	1.242	2.414
	Lambda	BHUG	1.832	0.301	1.242	2.422

Table 19: Asymptotic estimator summary statistics for individual-based sampling of birds at SHNGP using Chao estimators (see Gotelli and Ellison, 2013, and Chao et al. 2009). Results based on four survey points.

Habitat, Year	N	S_{obs}	f_1	f_2	Chao1	σ^2_{Chao}	Confidence Interval	n* (g=0.90)
UHG 2004	75	25	12	2	61	1116.0	(0,126)	1387
UHG 2012	91	25	6	6	28	10.5	(22,34)	159.5
UHG 2013	84	27	0	4	27	0.0	(27,27)	0
UHUG 2004	21	15	10	4	28	114.1	(7,49)	131
UHUG 2012	96	30	9	6	37	34.6	(25,49)	312
UHUG 2013	71	21	0	5	21	0.0	(21,21)	0
EX 2004	47	16	4	3	19	12.1	(12,26)	101
EX 2012	96	23	7	1	48	967.8	(0,109)	1909
EX 2013	65	21	0	4	21	0.0	(21,21)	0
BHG 2004	80	25	9	6	32	34.6	(20,44)	260
BHG 2012	109	30	10	6	38	47.7	(24,52)	416
BHG 2013	76	27	0	7	27	0.0	(27,27)	0
BHUG 2004	68	20	7	5	25	23.4	(16,34)	189
BHUG 2012	105	30	8	6	35	24.3	(25,45)	286
BHUG 2013	86	30	0	8	30	0.0	(30,30)	0

n = number of individuals collected in each treatment;

S_{obs} = number of observed species;

f_1 = number of singletons (species represented by one individual in sample);

f_2 = number of doubletons (species represented by exactly two individuals in sample);

Chao1 = estimate of species richness asymptote;

σ^2_{Chao} = variance of Chao1;

Confidence interval = parametric 95% confidence interval

n*(g=0.90) = estimated sampling number of additional individuals needed to reach 90% of Choa1; note that if there are no singletons, no additional sampling is required.

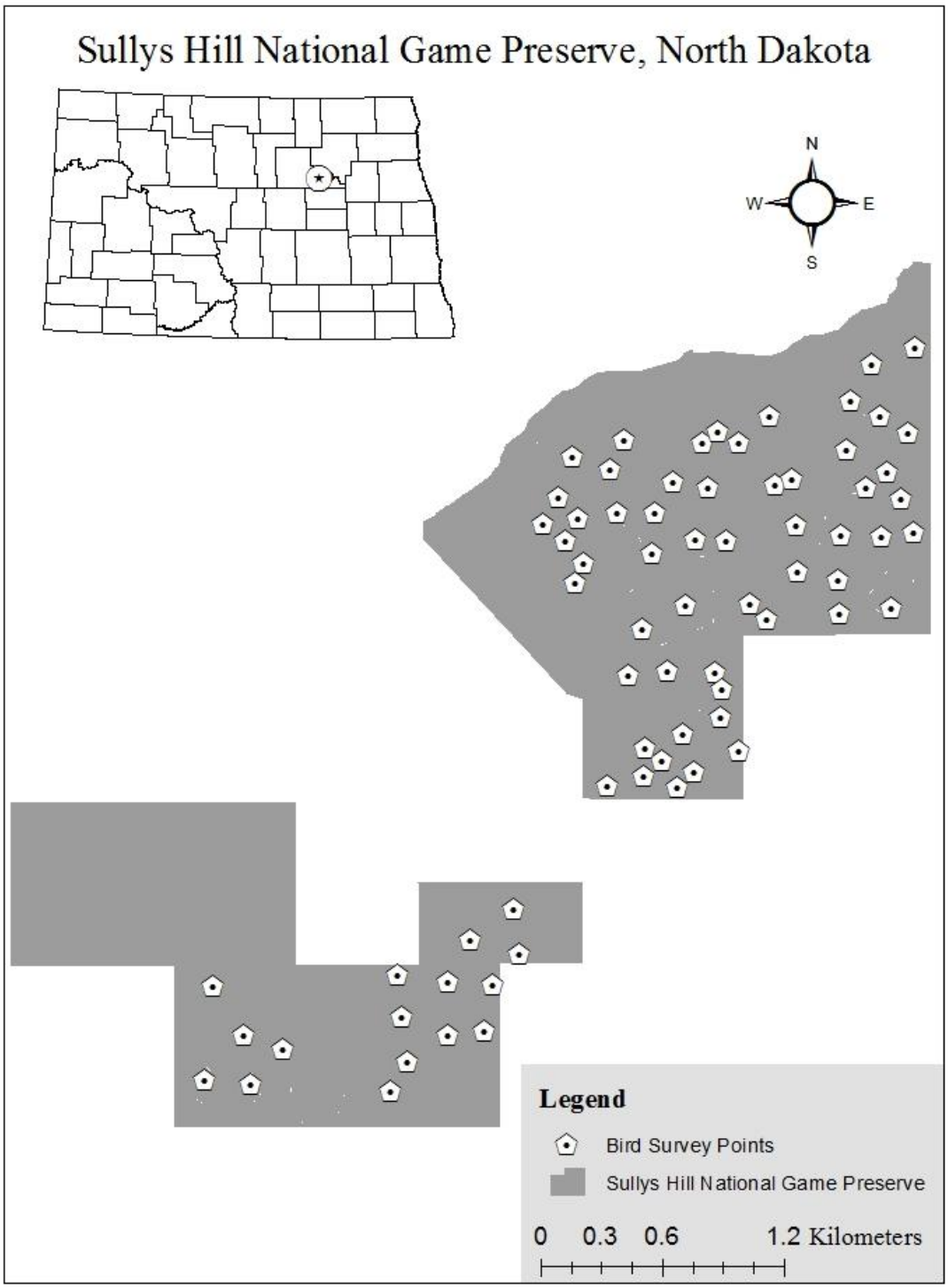
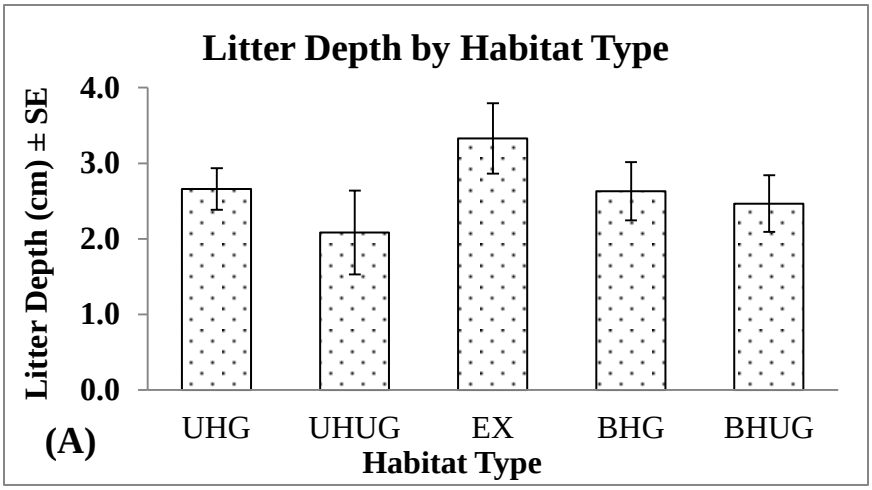
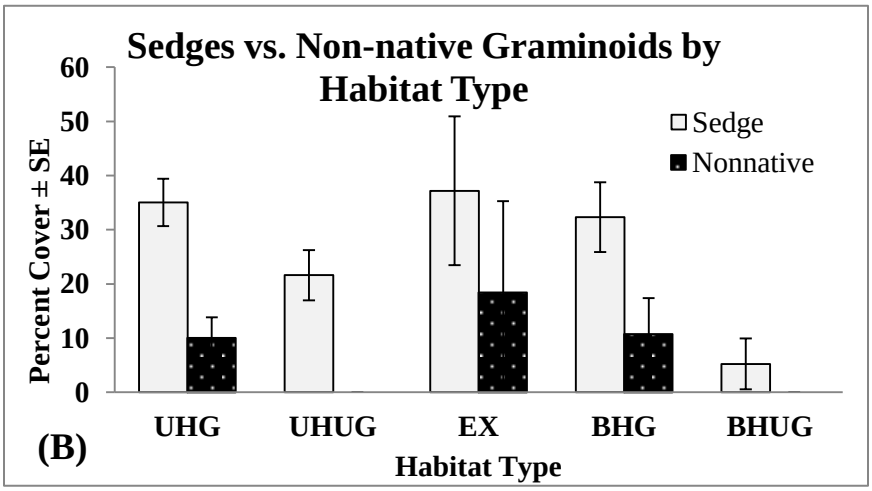


Figure 8: Avian point count survey locations at Sullys Hill National Game Preserve in North Dakota, 2012 – 2013.





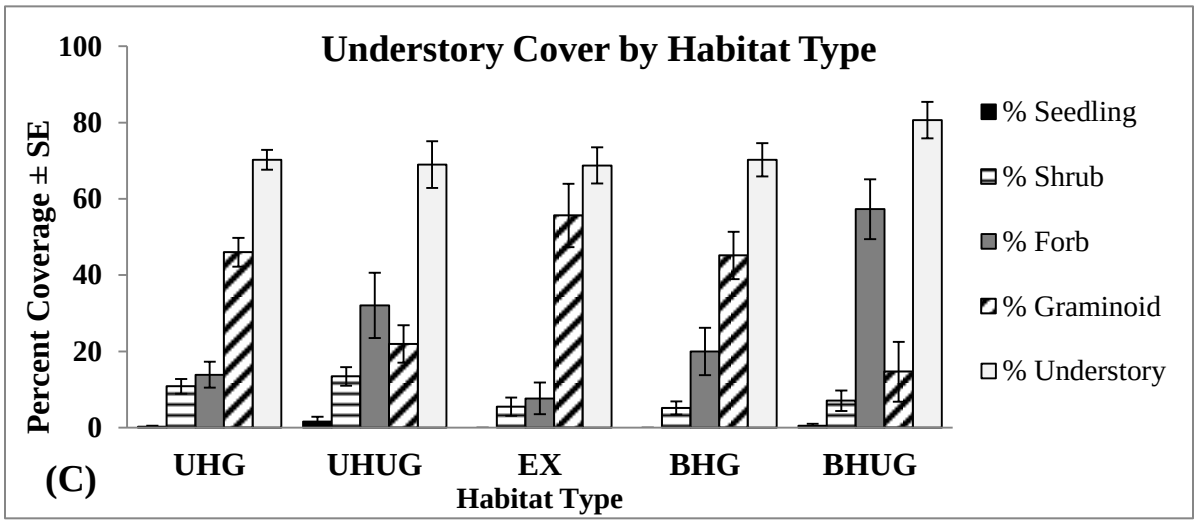


Figure 9: Understory metrics separated by habitat type for a) litter depth (cm), b) native sedges and non-native graminoids (Kentucky bluegrass and smooth brome) and c) percent vegetation for each habitat type.

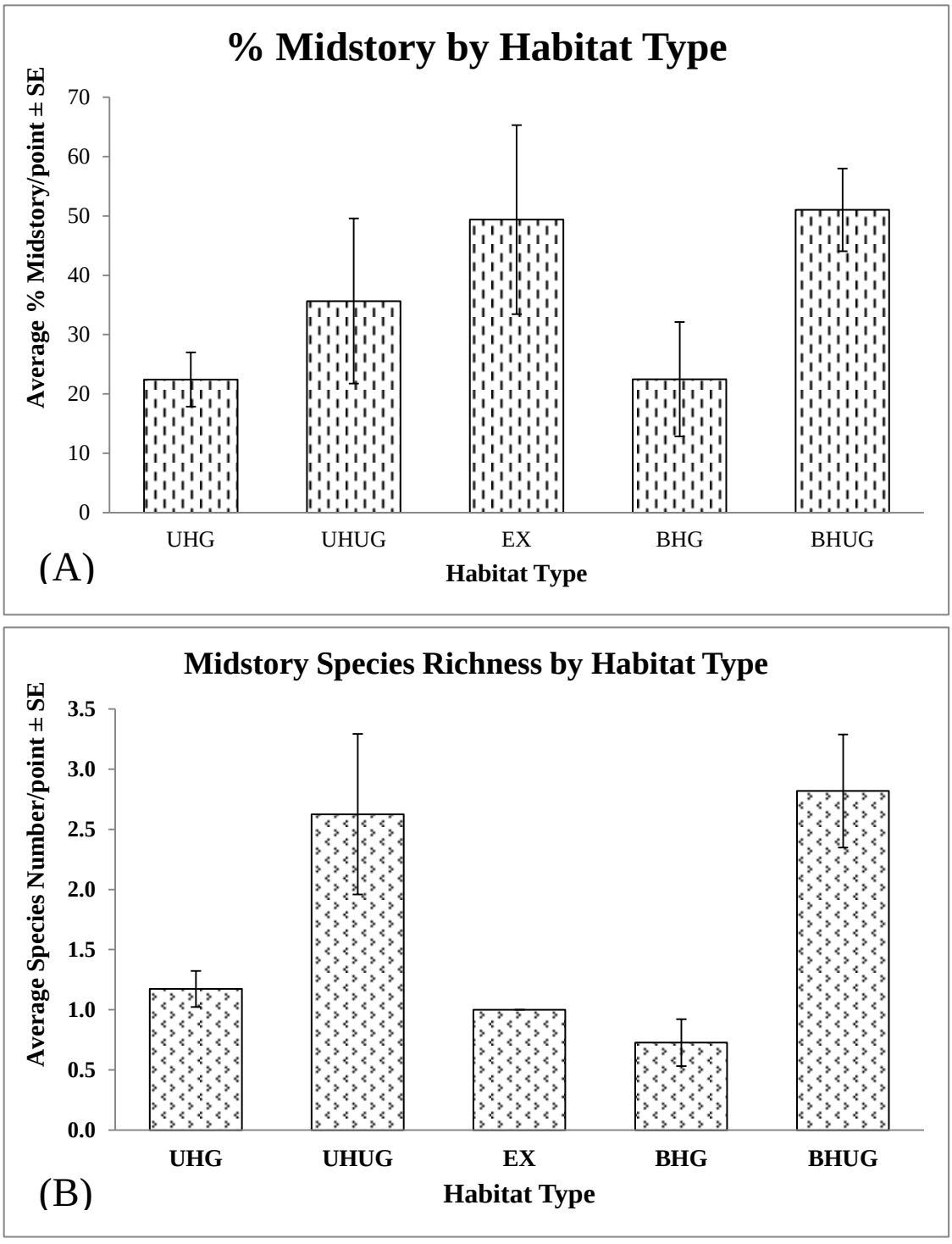


Figure 10: Midstory vegetation metrics of a) percent vegetation coverage at midstory level, and b) number of woody species at midstory level in each habitat type.

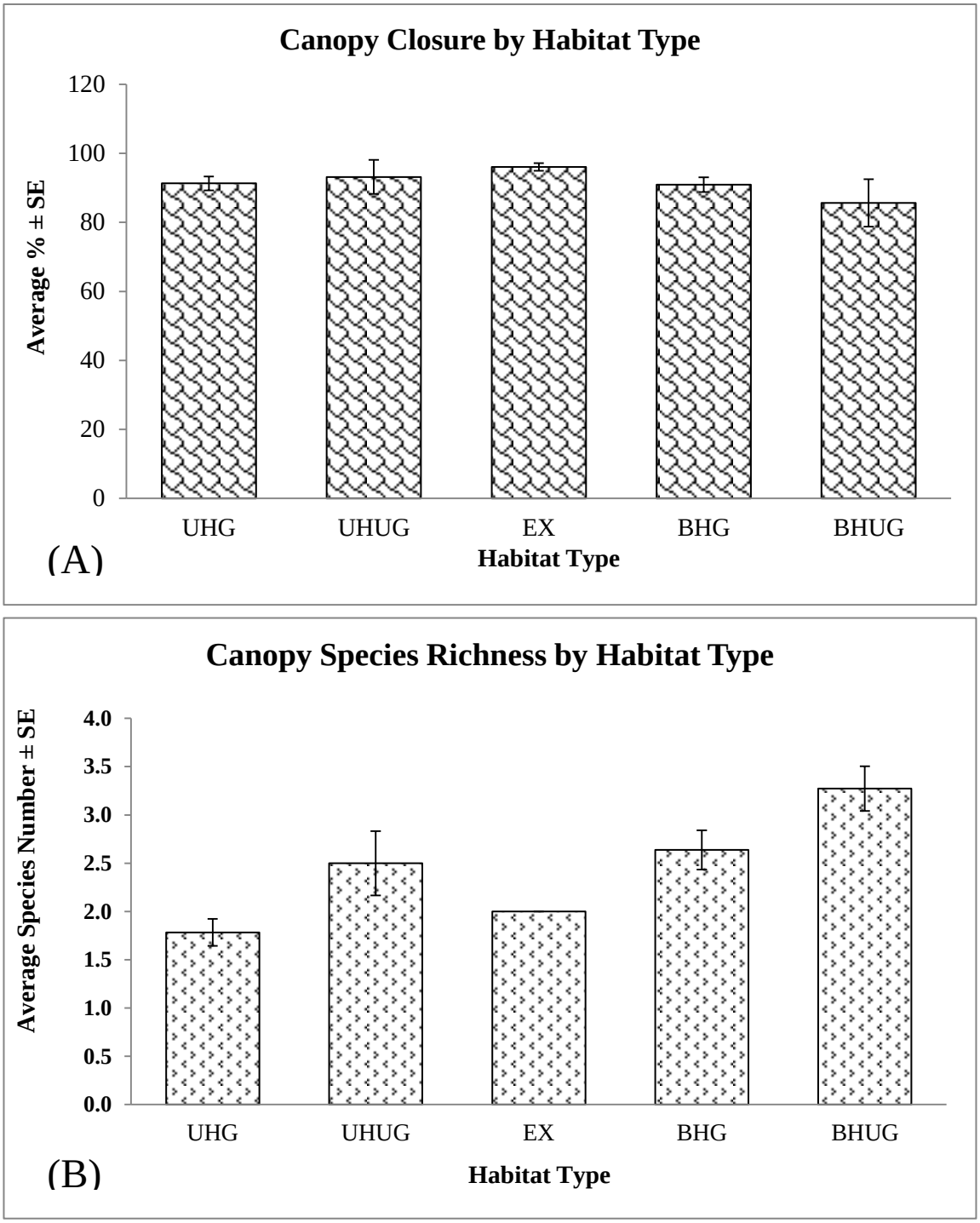


Figure 11: Canopy vegetation metrics of a) number of tree species in canopy of each habitat type, and b) percent canopy closure by habitat type.

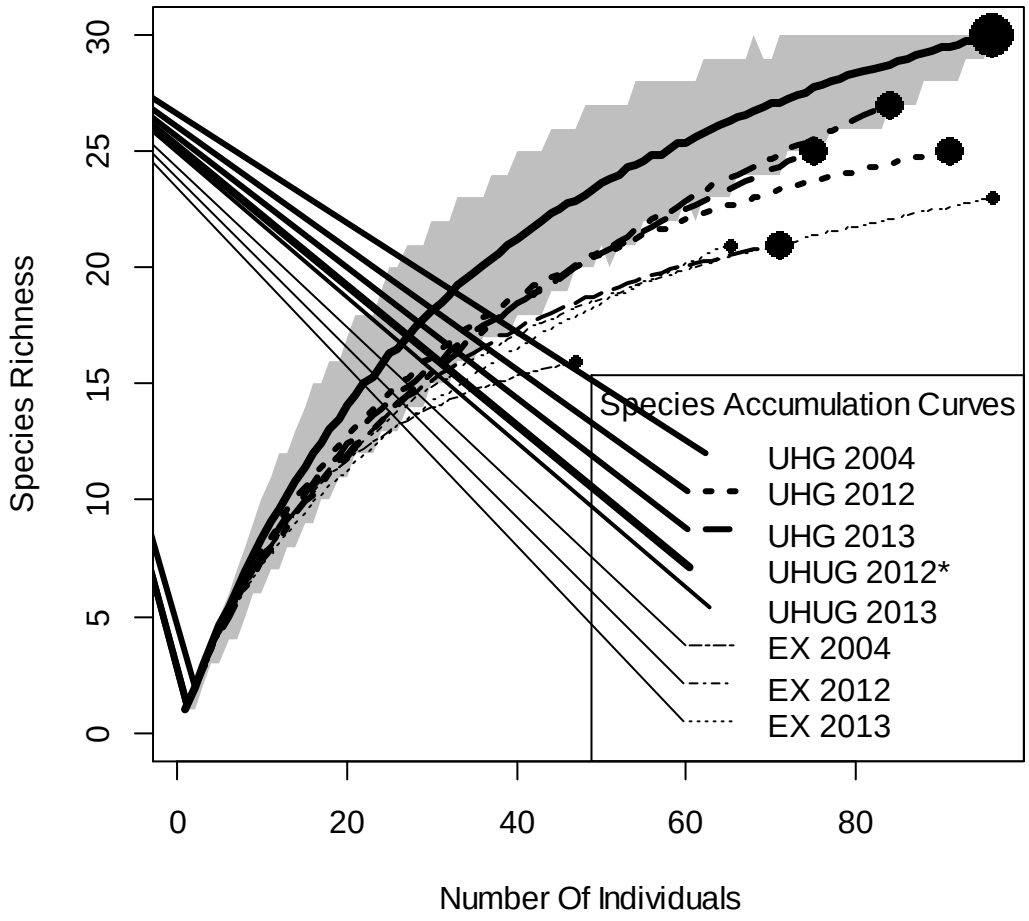


Figure 12: Individual-based species accumulation curves for bird species in upland habitat type and year (n=4). UHUG 2004 not included because n=1. *Baseline curve is UHUG 2012 and has 95% CI in gray.

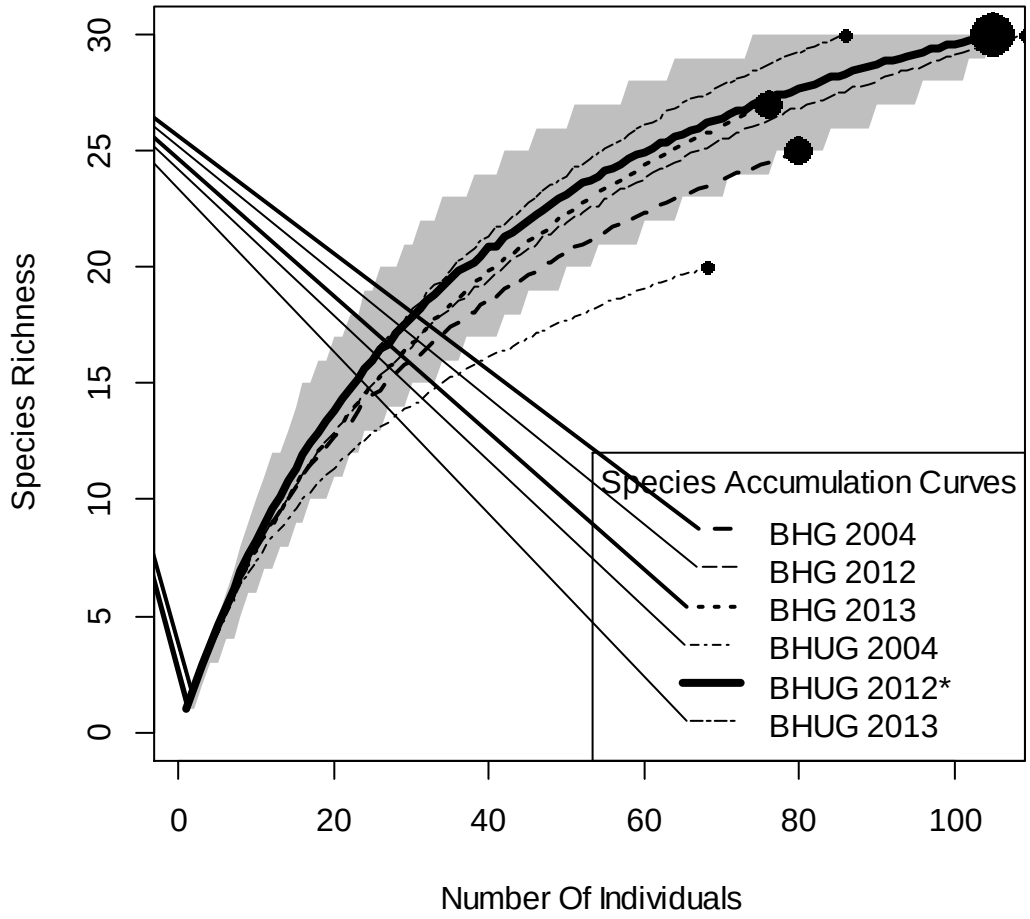


Figure 13: Individual-based species accumulation curves for bird species in bottomland habitat type and year (n=4). *Baseline curve is BHUG 2012 and has 95% CI in gray.

CHAPTER IV
CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The overarching goal of this two part project was to determine what effect ungulate herd reduction has had on forest regeneration and the associated bird community. The impetus for this study was suspected overbrowsing and subsequent destruction of forest habitat quality. This was confirmed by a forest survey conducted by North Dakota Forest Service (NDFS) in 2005 and a Subsequent management plan designed to reduce ungulate impact through culling. In addition to herd reduction, an exclosure was added on the recommendation of the NDFS to allow a 10.1 ha parcel to rest from browsing and grazing. Herds of Rocky Mountain elk (*Cervus elaphus*), Plains bison (*Bison bison*), and white-tailed deer (*Odocoileus virginianus*), reintroduced 1916-1918, had reached 40 animals/herd or a combined density of 37 ungulates/km^2 (23 AUM/km^2) by the late 1980's. Herd reduction in 2008 returned the density to that of 1941, 20 animals/herd or 19 ungulates/ km^2 (11 AUM/km^2).

Four years after herd reduction, we conducted a forest vegetation survey using the original NDFS protocol. Woody vegetation stems less than five cm were counted and speciated in 0.0004 ha plots at 70 survey points spread across grazed and ungrazed habitats (upland and bottomland hardwood) of SHNGP (Chapter 2). The objective was to find the amount of regeneration or seedling density in the grazed areas and compare to the ungrazed areas. We concluded that there was regeneration in the grazed areas, but it was below the regeneration found in ungrazed areas (Chapter 2). We used Chao estimators (Chao et al. 2009) to find maximum species numbers (asymptote of species accumulation curve) and species accumulation

curves to evaluate species richness. Results indicated that grazed areas had lower species richness, and increased species richness may require additional manipulations beyond the ungulate herd (Chapter 2). Based on these findings, future management objectives will need to build off of current objectives and address how to increase regeneration and species richness in the grazed areas of SNGHP. Based on Chao maximum species numbers we found that species richness for ungrazed bottomland had possibly peaked in 2005 and may be trending down (Chapter 2, Figure 8). This may be an indication that this area will need a disturbance treatment to maintain species richness (Petraitis et al. 1989, Hobbs and Huenneke 1992).

We also examined the possible effects of ungulates on bird populations through changes in vegetation (Chapter 3). Four target species, OVEN (*Seiurus aurocapilla*: hereafter OVEN), yellow warbler (*Dendroica petechia*: hereafter YEWA), American redstart (*Setophaga ruticilla*: herafter AMRE), and red-eyed vireo (*Vireo olivaceus*:hereafter REVI), were chosen to represent effects at different forest canopy layers. OVEN nest and forage in the understory, (Smith and Shugart 1987, Burke and Nol 1998, Seagle and Sturtevant 2005, Porneluzi et al. 2011); YEWA nest and forage in low midstory (McPeek and Adams 1994, Lowther et al. 1999, Campbell et al. 2001). AMRE nest and forage in midstory and low canopy (Lovette and Holmes 1995, Sherry and Holmes 1997), and REVI nest and forage in high midstory and canopy(James 1976, Cimprich et al. 2000). Avian surveys were conducted at 57 points across the SHNGP habitat types (Chapter 3). We evaluated effects on abundance due to lower browsing/grazing pressure and then we looked for possible relationships between the target bird species and vegetation structure, composition, and growth patterns. We found that only the OVEN showed changes in abundance between pre- and post-herd reduction, and those changes were only significant in

2012 demonstrating the annual variation in abundance that may be unrelated to ungulate herds (Chapter 3).

When we evaluated bird abundance relative to vegetation composition, we found that OVEN, YEWA, and AMRE showed biological trends or significant compositional relationships with vegetation. OVENs and YEWA were more abundant in shorter and less dense sedges over non-native bluegrass and smooth brome (Chapter 3). OVEN and YEWA abundance also was negatively impacted by forbs. AMRE and YEWA were in higher abundance in chokecherry stands such as those found in the exclosure (Teichman et al. 2013). We also noted higher abundance in OVEN with compositions of saplings such as basswood and elm. None of the vegetation covariates measured for canopy affected REVI abundance. Given the variety of responses observed among the four target birds, management will require approaches that increase or maintain habitat heterogeneity through structural diversity and vegetation species diversity (Haddad et al. 2011).

Disturbance options for forested areas include fire, grazing/browsing, thinning, and several harvest techniques (select cut, clear cut, coppice cut). Evaluation of these methods was beyond the scope of this project; however, research suggests the following three approaches as possible ways to increase or maintain heterogeneity across SHNGP: 1) Patch-burn-graze 2) small select cuts 3) coppice cuts.

Patch-burn-graze (PBG) plans involve small burns distributed throughout a larger area. Grazers such as bison prefer the vegetation of recently burned areas and will range between those burned areas (Allred et al. 2011). The advantages of this management tool include: 1) animals are distributed over larger areas and so reduce the impacts of repeated soil compaction (Bezkorowajnyj et al. 1993); 2) invasive grasses can be controlled first through timing of the

burn and second through continued browsing pressure (Grace et al. 2000, Harrod and Reichard 2000, Roy et al. 2014); 3) heterogeneity of the landscape is increased creating more opportunity for diverse plant-animal communities (Grimm 1984, Allred et al. 2011); 4) burning removes duff layers, increasing substrate diversity and allowing different seeds to germinate that require bare soil substrate (Nathan and Muller-Landau 2000).

PBG technique is usually applied to grasslands and differs from prescribed forest burns in objectives and size of burns (Ryan et al. 2013). Prescribed forest burns may involve as much as 1/3 of total area under management and the burns are on contiguous areas (USDA 1989, Wade and Lund 1990). PBG involves smaller patches, but could also be used for forest edges and interior openings where non-native grasses and forbs have become established. Although bison prefer open grassland to forested areas (Allred et al. 2011), they both graze and browse in forested areas. The more open oak savannah areas have historically depended on fire and could benefit through control of non-native grasses as well as removal of woody encroachment (Peterson and Reich 2001).

To promote regeneration of shade intolerant species, small select cuts can be used to create gaps in the canopy. This allows sunlight to penetrate the forest floor and can encourage germination, growth, and recruitment of shade intolerant tree and shrub species (Brokaw 1985). Techniques to increase regeneration are needed to improve the regeneration rates of the grazed areas. A return of midstory or structural diversity of midstory will encourage birds such as the target species of our study, YEWA and AMRE. With improved recruitment of shade tolerant and intolerant tree species, canopy bird species such as REVI may benefit from the structural diversity in the future (citation). This will increase structural heterogeneity of the forest and

again create opportunity for diversity of plant-animal communities (Brokaw 1985, Canham et al. 1990, Wright et al. 1998).

Another potential technique for improving regeneration involves coppice cuts or cutting a tree during a dormancy period and allowing saplings to grow from the base of the cut tree. This could accomplish two goals, more oak saplings and gaps in the canopy (Belanger 1979, Kirby 1990, Ducrey and Turrel 1992). Another advantage of coppice cutting is that it doesn't disturb the soil as much as other cutting techniques. This allows epiphytes, an important below ground community organism, to be maintained and will contribute more to the health and diversity of understory plants (Wolf 2005). AMRE abundance is lower in grazed areas and may increase with improved midstory density from this method (Chapter 3).

Managing ungulate numbers will have both direct and indirect effects on forest habitat (Côté et al. 2004). To manage for increases in tree regeneration and woody species diversity, there are benefits to reducing the number of browsers and treating grazing herds differently from those that browse. Bertie and Sweitzer (unpublished data) found deer diet consisted of trees and shrubs for fall and winter, with little hay utilization. Elk use trees and shrubs to supplement their diet in spring, summer, and fall. However, bison diet has almost no tree and shrub component (Figure 16), but affect woody midstory by horning and rubbing (Coppedge and Shaw 1997). This suggests that alternative ungulate herd management strategies may be appropriate.

In the Comprehensive Conservation Plan (CCP) of SHNGP, there is an alternate mixed ungulate density that has not been tried (USFWS 2008:45). The suggested densities for forest recovery are: 15 elk, 5 deer, and 19 bison. If reduction of browsers is combined with other management techniques such as PBG, the bison density may be increased and an increase in browsers may prove beneficial for the reasons noted above. This may be conditional on the

continued use of supplementary feeding. By continued use of supplemental feed, winter browsing by bison should be reduced (Kowalczyk et al. 2011), making the reduction of browsers species of elk and deer, more effective. The disadvantage of supplementary feeding is increased risk of disease transmission (Gortázar et al. 2006) and health of the animals (Putman and Staines 2004, Hines et al. 2007). Timing of supplementary feeding may be adjusted to encourage foraging behavior in bison. By waiting to supply feed until after snow fall, the animals will be forced to forage initially and might then rely less on supplementary feeding; however, there is no data other than anecdotal to support this.

In addition to implementing habitat management tools, monitoring of vegetation and birds at regular intervals and relative to management actions would benefit future decisions. Increased monitoring will allow for evaluations of management actions and the ability to discern how management actions impact the system temporally. We suggest repeating the forest surveys every four to five years to assess the regeneration status and the species richness of returning regeneration and keeping records of additional management actions relative to the sampling points. We suggest repeating bird surveys in a consistent protocol established by this study for 2-3 consecutive years periodically, if not annually, will better capture the stochasticity inherent in avian abundance due to climate and seasonality (e.g., 2012 and 2013 are example of extremes). With more data accumulated over the years, trends will be easier to find and less likely to be masked by annual variation. If the budget allows, we recommend a repeat of the detailed vegetation surveys with bird surveys, allowing a more comprehensive picture of the forest structure through time. Soil surveys may also be included to determine differences between upland and bottomland habitat and for comparison inside and outside animal enclosure.

Maintenance of Sullys Hill National Game Preserve (SHNGP) is vital because of the ungulates of historical importance kept there and because the "island" of forest habitat in the Devils Lake area may serve as a source of forest birds for the rest of the state (Robinson 1995).Our findings support small positive changes from ungulate reduction, but continued use of science-based management is needed to preserve this unique treasure in the Great Plains region.

LITERATURE CITED

Allred, B. W., S. D. Fuhlendorf, D. M. Engle, and R. D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire–grazing interaction. Ecology and Evolution 1:132-144.

Belanger, R. P. 1979. Stump management increases coppice yield of sycamore. Southern Journal of Applied Forestry 3:101-103.

Bezkorowajnyj, P., A. Gordon, and R. McBride. 1993. The effect of cattle foot traffic on soil compaction in a silvo-pastoral system. Agroforestry Systems 21:1-10.

Brokaw, N. V. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682-687.

Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. The Auk 115:96-104.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, A. C. Stewart, and M. C. McNall. 2001. The birds of British Columbia. Volume 4.British Columbia Museum, Victoria, British Columbia.

Canham, C. D., J. S. Denslow, W. J. Platt, J. R. Runkle, T. A. Spies, and P. S. White. 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20:620-631.

Chao, A., R. K. Colwell, C. W. Lin, and N. J. Gotelli. 2009. Sufficient sampling for asymptotic minimum species richness estimators. Ecology 90:1125-1133.

Cimprich, D. A., F. R. Moore, and M. P. Guilfoyle. 2000. Red-eyed vireo (*Vireo olivaceus*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 18 September 2012.

Coppedge, B. R., and J. H. Shaw. 1997. Effects of horning and rubbing behavior by bison (*Bison bison*) on woody vegetation in a tallgrass prairie landscape. American Midland Naturalist 138:189-196.

Côté, S. D., T. P. Rooney, J. P. Tremblay, C. Dussault, and D. M. Waller. 2004. Ecological impacts of deer overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113-147.

Ducrey, M., and M. Turrel. Influence of cutting methods and dates on stump sprouting in Holm oak (*Quercus ilex* L) coppice. EDP Sciences, 1992.

Gortázar, C., P. Acevedo, F. Ruiz-Fons, and J. Vicente. 2006. Disease risks and overabundance of game species. European Journal of Wildlife Research 52:81-87.

Grace, J.B., M.D. Smith, S.L. Grace, S.L. Collins, and T.J. Stohlgren. 2001. Interactions between fire and invasive plants in temperate grasslands of North America. Pages 40–65 in K.E.M. Galley and T.P. Wilson (eds.). Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire. Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

Grimm, E. C. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecological Monographs 54:291-311.

Haddad, N. M., G. M. Crutsinger, K. Gross, J. Haarstad, and D. Tilman. 2011. Plant diversity and the stability of foodwebs. Ecology Letters 14:42-46.

Harrod, R.J., and S. Reichard. 2001. Fire and invasive species within the temperate and boreal coniferous forests of western North America. Pages 95–101 in K.E.M. Galley and T.P. Wilson (eds.). Proceedings of the Invasive Species Workshop: the Role of Fire in the Control and Spread of Invasive Species. Fire Conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, FL.

Hines, A. M., V. O. Ezenwa, P. Cross, and J. D. Rogerson. 2007. Effects of supplemental feeding on gastrointestinal parasite infection in elk (*Cervus elaphus*): Preliminary observations. Veterinary Parasitology 148:350-355.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6:324-337.

James, R. D. 1976. Foraging behavior and habitat selection of three species of vireos in southern Ontario. The Wilson Bulletin 88:62-75.

Kirby, K. J. 1990. Changes in the Ground Flora of a Broadleaved Wood within a Clear Fell, Group Fells and a Coppiced Block. Forestry 63:241-249.

Kowalczyk, R., P. Taberlet, E. Coissac, A. Valentini, C. Miquel, T. Kamiński, and J. M. Wójcik. 2011. Influence of management practices on large herbivore diet—Case of European bison in Białowieża Primeval Forest (Poland). Forest Ecology and Management 261:821-828.

Lovette, I. J., and R. T. Holmes. 1995. Foraging behavior of American Redstarts in breeding and wintering habitats: implications for relative food availability. Condor 97:782-791.

Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. 1999. Yellow warbler (*Setophaga petechia*). The Birds of North America Online (A. Poole, Ed.). Ithaca:

Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 19 September 2012.

McPeek, G. A., and R. J. Adams. 1994. The birds of Michigan. Indiana University Press. Indianapolis, Indiana, USA.

Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15:278-285.

Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecological Applications 11:914-927.

Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. Quarterly Review of Biology:393-418.

Porneluzi, P., M. A. Van Horn, and T. M. Donovan. 2011. Oven Bird (*Seiurus aurocapilla*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 9 September 2012.

Putman, R. J., and B. W. Staines. 2004. Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. Mammal Review 34:285-306.

Robinson, S. K., Thompson III, F.R. Donovan, T.M, Whitehead, D.R. Faaborg, John. 1995. Regional forest fragmentation and the nesting success of migratory birds. Science 267:93-102.

Roy, B. A., K. Hudson, M. Visser, and B. R. Johnson. 2014. Grassland fires may favor native over introduced plants by reducing pathogen loads. Ecology 95:1897-1906.

Ryan, K. C., E. E. Knapp, and J. M. Varner. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Frontiers in Ecology and the Environment 11:e15-e24.

Seagle, S. W., and B. R. Sturtevant. 2005. Forest productivity predicts invertebrate biomass and ovenbird (*Seiurus aurocapillus*) reproduction in Appalachian landscapes. Ecology 86:1531-1539.

Sherry, T. W., and R. T. Holmes. 1997. American redstart (*Setophaga ruticilla*). The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology. http://bna.birds.cornell.edu/bna/. Accessed 20 September 2012.

Smith, T. M., and H. H. Shugart. 1987. Territory size variation in the ovenbird: the role of habitat structure. Ecology 68:695-704.

Teichman, K. J., S. E. Nielsen, and J. Roland. 2013. Trophic cascades: linking ungulates to shrub-dependent birds and butterflies. Journal of Animal Ecology 82:1288-1299.

USDA Forest Service, U. F. 1989. Reasons for Prescribed Fire in Forest Resource Management. Technical Publications R8-TP 11, University of Georgia, Warnell School of Forestry and Natural Resources. http://www.bugwood.org/pfire/reasons.html. Accessed 24 November 2014

Wade, D. D., and J. Lundsford. 1990. Fire as a forest management tool: prescribed burning in the southern United States. Unasylva 41:28-38.

Wolf, J. H. 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management 212:376-393.

Wright, E. F., K. D. Coates, and P. Bartemucci. 1998. Regeneration from seed of six tree species in the interior cedar-hemlock forests of British Columbia as affected by substrate and canopy gap position. Canadian Journal of Forest Research 28:1352-1364.

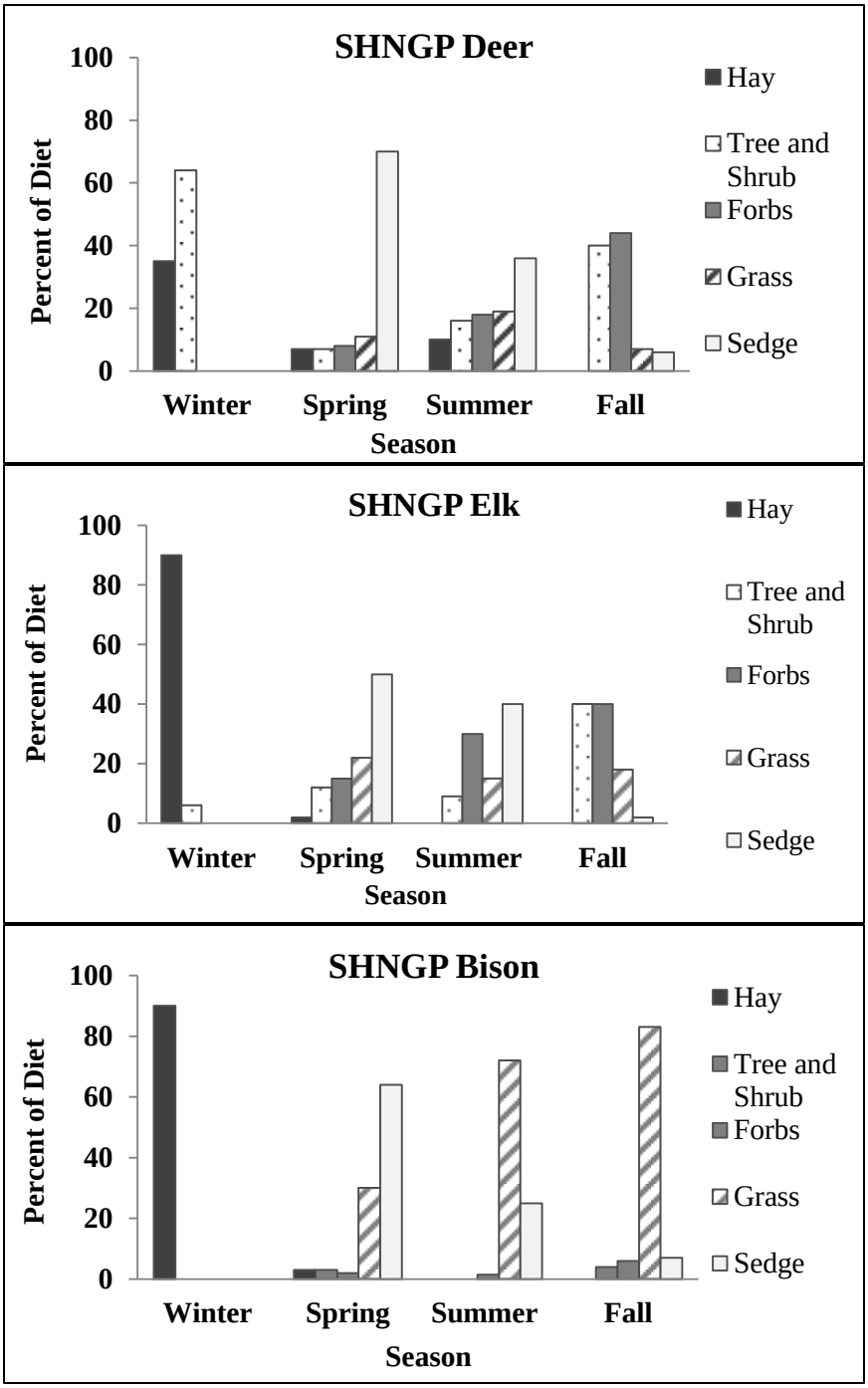


Figure 14: Percent of diet of each vegetation across four seasons of sampling (Reproduced from Bertie and Sweitzer unpublished data).

APPENDICES

Table 20: Parameter estimates and 95% confidence interval (CI) for all eleven models used to evaluate stem density. Output is from SAS. Stem density was the response variable; treatment, year, and habitat were the covariates used to produce models. The best model based on weighted Akaike scores: Stem density = $\beta + \beta(\text{Treatment}) + \beta(\text{Year}) + \beta(\text{Habitat}) + \theta$. Dispersion factor = θ

Model		Estimate	SE	LCI	UCI	AICc	Deviance	GOF
Treatment + Year + Habitat						763.5	59.984	0.983
	Intercept	6.846	0.789	5.299	8.392			
	Treatment	-3.037	0.919	-4.838	-1.236			
	Year	2.234	0.926	0.419	4.050			
	Habitat	1.558	0.921	-0.247	3.362			
	Dispersion	8.884	1.733	6.062	13.022			
Treatment + Year						764.3	59.984	0.968
	Intercept	7.771	0.756	6.290	9.253			
	Treatment	-2.591	0.816	-4.190	-0.991			
	Year	1.572	0.763	0.076	3.068			
	Dispersion	9.423	1.826	6.446	13.777			
Treatment						765.7	60.001	0.952
	Intercept	8.783	0.693	7.424	10.142			
	Treatment	-2.495	0.843	-4.147	-0.843			
	Dispersion	10.097	1.942	6.926	14.721			
Year						771.7	60.069	0.954
	Intercept	6.864	0.593	5.701	8.026			
	Year	1.415	0.833	-0.217	3.047			
	Dispersion	11.259	2.143	7.753	16.349			
Intercept (Null)						772.1	60.122	0.939
	Intercept	7.812	0.426	6.977	8.647			
	Dispersion	11.796	2.235	8.137	17.102			

Table 20 Continued

Model		Estimate	SE	LCI	UCI	AICc	Deviance	GOF
Habitat*Year						772.2	60.077	0.954
	Intercept	7.341	0.472	6.415	8.266			
	Habitat*Year	1.335	1.017	-0.659	3.329			
	Dispersion	11.367	2.162	7.830	16.501			
Treatment*Year						772.6	60.085	0.954
	Intercept	8.093	0.516	7.082	9.104			
	Treatment*Year	-1.281	0.886	-3.018	0.457			
	Dispersion	11.440	2.174	7.882	16.603			
Habitat*Treatment						772.7	60.843	0.954
	Intercept	8.041	0.494	7.073	9.009			
	Habitat*Treatment	-1.338	0.939	-3.178	0.502			
	Dispersion	11.466	2.179	7.901	16.640			
Habitat + Year						772.7	60.053	0.969
	Intercept	0.682	0.694	5.021	7.743			
	Habitat	0.871	0.833	-0.761	2.503			
	Year	1.440	0.825	-0.177	3.056			
	Dispersion	11.038	2.105	7.596	16.039			
Habitat						773.3	60.095	0.954
	Intercept	7.366	0.560	6.269	8.463			
	Habitat	0.836	0.853	-0.836	2.508			
	Dispersion	11.596	2.201	7.994	16.823			
Habitat*Treatment*Year						773.9	60.106	0.954
	Intercept	7.891	0.458	6.994	8.787			
	Habitat*Treatment*Year	-0.782	1.230	-3.193	1.628			
	Dispersion	11.728	2.224	8.088	17.008			

Table 21: Abundance models constructed using ovenbird abundance data from 2012 and 2013. Data from 57 points was used in this analysis. See Table 3, Chapter 3, in bird chapter for covariate descriptions

Model	K	AICc	ΔAICc	w	L	Deviance
r (sarsap) λ (native forb+blue+brome+mbass)	7.00	378.85	0.00	0.39	1.00	363.79
r (sarsap) λ (native forb+blue+brome+mbass+canopy)	8.00	380.64	1.79	0.16	0.41	363.27
r (sarsap) (native forb+blueλ+brome+mbass+melm)	8.00	381.04	2.19	0.13	0.33	363.67
r (sarsap) λ (mbass)	4.00	382.20	3.35	0.07	0.19	373.84
r (sarsap) λ (blue+brome)	5.00	382.91	4.06	0.05	0.13	372.35
r (sarsap) λ (brome)	4.00	383.19	4.34	0.04	0.11	374.83
r (sarsap) λ (melm)	4.00	384.40	5.55	0.02	0.06	376.03
r (sarsap) λ (native forb)	4.00	384.73	5.88	0.02	0.05	376.36
r (sarsap) λ (canopy)	4.00	385.46	6.61	0.01	0.04	377.10
r (sarsap) λ (blue)	4.00	385.54	6.69	0.01	0.04	377.18
r (sarsap) λ (.)	3.00	385.58	6.73	0.01	0.03	379.36
r (sarsap) λ (sarsap)	4.00	386.07	7.22	0.01	0.03	377.70
r (sarsap) λ (sedge)	4.00	386.33	7.48	0.01	0.02	377.96
r (sarsap) λ (understory)	4.00	386.36	7.51	0.01	0.02	377.99
r (sarsap) λ (litter)	4.00	386.71	7.86	0.01	0.02	378.34
r (sarsap) λ (midstory)	4.00	386.76	7.91	0.01	0.02	378.39
r (sarsap) λ (midstory spp #)	4.00	386.78	7.93	0.01	0.02	378.42
r (sarsap) λ (exclosure+grazed)	5.00	386.93	8.08	0.01	0.02	376.37
r (sarsap) λ (bottom)	4.00	387.18	8.33	0.01	0.02	378.81
r (sarsap) λ (shrub)	4.00	387.46	8.61	0.01	0.01	379.09
r (sarsap) λ (year)	4.00	387.56	8.71	0.00	0.01	379.19
r (understory) λ (.)	3.00	395.10	16.25	0.00	0.00	388.88
r (canopy) λ (.)	3.00	396.53	17.68	0.00	0.00	390.31
r (.) λ (.)	2.00	397.82	18.97	0.00	0.00	393.71
r (year) λ (.)	3.00	397.87	19.02	0.00	0.00	391.65
r (ex+grazed) λ (.)	4.00	397.87	19.02	0.00	0.00	389.51
r (shrub) λ (.)	3.00	398.36	19.51	0.00	0.00	392.14
r (midstory) λ (.)	3.00	399.33	20.48	0.00	0.00	393.11
r (g) λ (.)	6.00	402.18	23.33	0.00	0.00	389.40
r (g) λ (g)	10.00	406.21	27.36	0.00	0.00	384.07

Table 22: Abundance models constructed using yellow warbler data from 2012 and 2013. Data from 57 points was used in this analysis. See Table 3, Chapter 3, in bird chapter for covariate descriptions.

Model	K	AICc	ΔAICc	w	L	Deviance
r (year) λ (bottom + litter + sarsap + midstory)	7	1034.05	0.00	0.25	1.00	1018.99
r (year) λ (sarsap + forb + midstory)	6	1034.85	0.80	0.17	0.67	1022.06
r (year) λ(litter + sarsap + midstory + mbass)	7	1035.03	0.98	0.15	0.61	1019.97
r (year) λ(litter + sarsap + forb + midstory)	7	1035.11	1.06	0.15	0.59	1020.05
r (year) λ (forbs)	4	1035.31	1.26	0.13	0.53	1026.94
r (year) λ (midstory)	4	1038.22	4.17	0.03	0.12	1029.85
r (year) λ (sarsap)	4	1038.36	4.31	0.03	0.12	1029.99
r (year) λ (litter+sedge+brome)	6	1039.61	5.56	0.02	0.06	1026.82
r (year) λ (litter+sedge)	5	1040.26	6.21	0.01	0.04	1029.70
r (year) λ (litter)	4	1040.47	6.42	0.01	0.04	1032.11
r (year) λ (sedge)	4	1041.13	7.08	0.01	0.03	1032.76
r (year) λ (mbass)	4	1041.16	7.11	0.01	0.03	1032.79
r (year) λ (bottom)	4	1041.19	7.14	0.01	0.03	1032.83
r (year) λ (litter+sedge+blue +brome)	7	1041.88	7.83	0.01	0.02	1026.82
r (year) λ (litter+sedge+blue)	6	1042.45	8.40	0.00	0.02	1029.66
r (year) λ (.)	3	1043.87	9.82	0.00	0.01	1037.65
r (year) λ (understory)	4	1044.12	10.07	0.00	0.01	1035.75
r (exclosure+grazed) λ (.)	4	1044.43	10.38	0.00	0.01	1036.06
r (year) λ (brome)	4	1044.80	10.75	0.00	0.00	1036.43
r (year) λ (canopy)	4	1044.83	10.78	0.00	0.00	1036.46
r (year) λ (blue)	4	1045.03	10.98	0.00	0.00	1036.66
r (midstory) λ (.)	3	1045.18	11.13	0.00	0.00	1038.96
r (.) λ (.)	2	1045.31	11.26	0.00	0.00	1041.20
r (year) λ (mhazel)	4	1046.00	11.95	0.00	0.00	1037.64
r (g) λ (.)	6	1048.11	14.06	0.00	0.00	1035.32

Table 23: Abundance models constructed using American redstart data from 2012 and 2013. Data from 57 points was used in this analysis. See Table 3, in bird chapter for covariate description.

Model	K	AICc	ΔAICc	w	L	Deviance
r (g) λ (year + litter + understory + midstory + mash + mhazel + canopy)	13	512.53	0.00	0.99	1.00	514.53
r (g) λ (litter + midstory + mhazel + canopy)	10	523.01	10.48	0.01	0.01	525.01
r (g) λ (midstory+mash+mhazel)	9	524.92	12.39	0.00	0.00	526.92
r (g) λ (year+understory+mash)	9	527.98	15.45	0.00	0.00	529.98
r (g) λ (mash)	7	529.61	17.08	0.00	0.00	531.61
r (g) λ (understory)	7	529.86	17.32	0.00	0.00	531.86
r (g) λ (litter)	7	532.06	19.53	0.00	0.00	534.06
r (g) λ (midstory)	7	532.87	20.34	0.00	0.00	534.87
r (g) λ (mhazel)	7	533.02	20.49	0.00	0.00	535.02
r (g) λ (canopy)	7	534.19	21.66	0.00	0.00	536.19
r (g) λ (year)	7	534.44	21.91	0.00	0.00	536.44
r (g) λ (.)	6	535.71	23.18	0.00	0.00	537.71
r (ex+grazed) λ (.)	4	541.46	28.92	0.00	0.00	543.46
r (midstory) λ (.)	3	554.40	41.87	0.00	0.00	556.40
r (canopy) λ (.)	3	594.60	82.06	0.00	0.00	596.60
r (year) λ (.)	3	594.67	82.14	0.00	0.00	596.67
r (.) λ (.)	2	594.78	82.25	0.00	0.00	596.78

Table 24: Avian species with alpha codes, common name, and scientific name and presence (x) or absence (0) in 2004, 2012, and 2013.

Species	Common Name	Scientific Name	2004	2012	2013
AMCR	American Crow	*Corvus brachyrhynchos*	x	x	x
AMGO	American Goldfinch	*Spinus tristis*	x	x	x
AMRE	American Redstart	*Setophaga ruticilla*	x	x	x
AMRO	American Robin	*Turdus migratorius*	x	x	x
BAOR	Baltimore Oriole	*Icterus galbula*	0	x	x
BEKI	Belted Kingfisher	*Megaceryle alcyon*	0	x	x
BAWW	Black & White Warbler	*Mniotilta varia*	x	x	x
BBCU	Black-billed Cuckoo	*Coccyzus erythropthalmus*	0	x	x
BCCH	Black-capped Chickadee	*Poecile atricapillus*	x	x	x
BCNH	Black-crowned Night Heron	*Nycticorax nycticorax*	0	x	x
BLJA	Bluejay	*Cyanocitta cristata*	x	x	x
BWHA	Broad-winged Hawk	*Buteo platypterus*	0	x	x
BRCR	Brown Creeper	*Certhia americana*	0	x	0
BHCO	Brown-headed Cowbird	*Molothrus ater*	x	x	x
CEWA	Cedar Waxwing	*Bombycilla cedrorum*	x	x	x
CCSP	Clay-colored Sparrow	*Spizella pallida*	x	x	x
CHSP	Chipping Sparrow	*Spizella passerina*	x	x	x
COYE	Common Yellowthroat	*Geothlypis trichas*	x	x	x
COHA	Coopers Hawk	*Accipiter cooperii*	x	0	0
DOWO	Downy Woodpecker	*Picoides pubescens*	x	x	x
EABL	Eastern Bluebird	*Sialia sialis*	x	x	x
EAKI	Eastern Kingbird	*Tyrannus tyrannus*	x	x	x
EATO	Eastern Towhee	*Pipilo erythrophthalmus*	0	x	x
EAWP	Eastern Wood-peawee	*Contopus virens*	x	x	x
FISP	Field Sparrow	*Spizella pusilla*	x	0	x
GRCA	Grey Catbird	*Dumetella carolinensis*	x	x	x
GCFL	Great-creasted Flycatcher	*Myiarchus crinitus*	x	x	x
HAWO	Hairy Woodpecker	*Picoides villosus*	x	x	x
HOME	Hooded Merganzer	*Lophodytes cucullatus*	0	0	x
HOWR	House Wren	*Troglodytes aedon*	x	x	x
INBU	Indigo Bunting	*Passerina cyanea*	x	0	0
KILL	Killdeer	*Charadrius vociferus*	0	x	x
LASP	Lark Sparrow	*Chondestes grammacus*	x	0	x
LEFL	Least Flycatcher	*Empidonax minimus*	x	x	x
MALL	Mallard	*Anas platyrhynchos*	x	0	x

Table 24 continued.

Species	Common Name	Scientific Name	2004	2012	2013
MAWR	Marsh Wren	*Cistothorus palustris*	0	0	x
MODO	Mourning Dove	*Zenaida macroura*	0	x	x
NOFL	Northern Flicker	*Colaptes auratus*	0	x	x
NOWA	Northern Waterthrush	*Parkesia noveboracensis*	0	x	x
OVEN	Ovenbird	*Seiurus aurocapilla*	x	x	x
PIWO	Pileated Woodpecker	*Dryocopus pileatus*	0	x	x
RBWO	Red-bellied woodpecker	*Melanerpes carolinus*	0	x	x
REVI	Red-eyed Vireo	*Vireo olivaceus*	x	x	x
RTHA	Red-tailed Hawk	*Buteo jamaicensis*	0	x	0
RWBL	Red-winged Blackbird	*Agelaius phoeniceus*	x	x	x
RBGR	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	0	x	x
RTHU	Ruby-throated Hummingbird	*Archilochus colubris*	0	x	x
SEWR	Sedge Wren	*Cistothorus platensis*		0	x
SOSP	Sharp-Shinned Hawk	*Accipiter striatus*	0	x	x
SSHA	Song Sparrow	*Melospiza melodia*	x	x	x
TRES	Tree Swallow	*Tachycineta bicolor*	x	x	x
VEER	Veery	*Catharus fuscescens*	x	x	x
VESP	Vesper Sparrow	*Pooecetes gramineus*	0	x	0
WAVI	Warbling Vireo	*Vireo gilvus*		0	x
WBNU	White-breasted Nuthatch	*Sitta carolinensis*	x	x	x
WODO	Woodduck	*Aix sponsa*		0	x
YEWA	Yellow Warbler	*Setophaga petechia*	x	x	x
YBCU	Yellow-billed Cuckoo	*Coccyzus americanus*		0	x
YBSA	Yellow-bellied Sapsucker	*Sphyrapicus varius*	x	x	x
YHBL	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*	x	0	0
YTVI	Yellow-throated Vireo	*Vireo flavifrons*	x	x	x
		Total Species Observed =	114	173	169

Table 25: Incidental avian sightings at Sullys Hill National Game Preserve, not observed at survey points. Most species are migrating through or on wetlands.

Date	Alpha Code	Common Name	Scientific Name
5/27/2004	TEWA	Tennessee Warbler	*Oreothlypis peregrine*
5/20/2012	WISN	Wilson's Snipe	*Gallinago delicate*
	GHOW	Great Horned Owl	*Bubo virginianus*
	NAWA	Nashville Warble	*Oreothlypis ruficapilla*
5/21/2012	CANG	Canada Goose	*Branta Canadensis*
	GBHE	Great Blue Heron	*Ardea Herodias*
	GREG	Great Egret	*Ardea alba*
	SWTH	Swainson's Thrush	*Catharus ustulatus*
5/22/2012	AMBI	American Bittern	*Botaurus lentiginosus*
5/25/2012	BLPW	Blackpoll Warbler	*Setophaga striata*
	YRWA	Yellow-rumped Warbler	*Setophaga coronate*
	ALFL	Alder Flycatcher	*Empidonax alnorum*
5/30/2012	SCTA	Scarlet Tanager	*Piranga olivacea*
	STGR	Sharp-tailed Grouse	*Tympanuchus phasianellus*
	YBFL	Yellow-bellied Flycatcher	*Empidonax flaviventris*
6/4/2012	OROR	Orchard Oriole	*Icterus spurius*
6/11/2012	WAVI	Warbling Vireo	*Warbling Vireo*
	EAPH	Eastern Phoebe	*Sayornis phoebe*
7/3/2012	TUVU	Turkey Vulture	*Cathartes aura*
7/5/2012	COGR	Common Grackle	*Quiscalus quiscula*
5/27/2013	MAWA	Magnolia Warbler	*Setophaga magnolia*
	MOWA	Mourning Warbler	*Geothlypis Philadelphia*
6/3/2013	PISI	Pine Siskin	*Spinus pinus*
	HETH	Hermit Thrush	*Catharus guttatus*
	CSWA	Chestnut-sided Warbler	*Setophaga pensylvanica*
6/6/2013	SPSA	Spotted Sandpiper	*Actitis macularius*
6/7/2013	DCCO	Double-crested Cormorant*	*Phalacrocorax auritus*
	CORA	Common Raven	*Corvus corax*
6/11/2013	INBU	Indigo Bunting	*Passerina cyanea*
	EAME	Eastern Meadowlark	*Sturnella magna*
6/15/2013	LARB	Lark Bunting	*Calamospiza melanocorys*
6/19/2013	BUFF	Bufflehead	*Bucephala albeola*
	LASP	Lark Sparrow	*Chondestes grammacus*
6/6/2013	BRTH	Brown Thrasher	*Toxostoma rufum*
6/30/2013	SORA	Sora	*Porzana Carolina*
7/7/2013	WTSP	White-throated Sparrow	*Zonotrichia albicollis*

*Nesting colony on Sweetwater Lake inside SHNGP

Table 26: Abundance models based on red-eyed vireo 2012/2013 data. Data from 57 points used to construct models. See Table 3, chapter 3 for description of covariates.

Model	AICc	ΔAICc	w	L	K	Deviance
r (canopy) λ (year)	708.84	0.00	0.20	1.00	4	700.48
r (canopy) λ (year+canopy)	709.98	1.14	0.11	0.57	5	699.43
r (canopy) λ (.)	710.09	1.24	0.11	0.54	3	703.87
r (canopy) λ (year+bottom)	711.00	2.16	0.07	0.34	5	700.45
r (canopy) λ (year+litter)	711.02	2.17	0.07	0.34	5	700.46
r (year) λ (.)	711.06	2.22	0.07	0.33	3	704.84
r (canopy) λ (canopy spp #)	711.53	2.68	0.05	0.26	4	703.16
r (canopy) λ (understory)	711.60	2.76	0.05	0.25	4	703.23
r (.) λ (.)	711.90	3.06	0.04	0.22	2	707.79
r (canopy) λ (midstory)	712.08	3.24	0.04	0.20	4	703.71
r (canopy) λ (bottom)	712.21	3.37	0.04	0.19	4	703.84
r (canopy) λ (litter)	712.22	3.38	0.04	0.18	4	703.86
r (canopy) λ (year+exclosure+grazed)	712.62	3.78	0.03	0.15	6	699.84
r (.) λ (canopy)	712.92	4.08	0.03	0.13	3	706.70
r (canopy) λ (litter+canopy)	713.46	4.62	0.02	0.10	5	702.91
r (canopy) λ (ex+grazed)	713.81	4.96	0.02	0.08	5	703.25
r (midstory) λ (.)	714.01	5.17	0.01	0.08	3	707.79
r (canopy) λ (canopy+exclosure+grazed)	715.21	6.36	0.01	0.04	6	702.42
r (canopy) λ (litter+exclosure+grazed)	715.96	7.12	0.01	0.03	6	703.17
r (ex+ed) λ (.)	716.02	7.17	0.01	0.03	4	707.65
r (g) λ (.)	716.92	8.08	0.00	0.02	6	704.14
r (.) λ (g)	718.30	9.46	0.00	0.01	6	705.52